Isotopic paleoecology ($\delta^{13}C$, $\delta^{18}O$) of late Quaternary herbivorous mammal assemblages from southwestern Amazon

Lidiane Asevedo[1,2*], Alceu Ranzi[3], Risto Kalliola[4], Martti Parssinen[5], Kalle Ruokolainen[6], Mário Alberto Cozzuol[7], Ednair Rodrigues do Nascimento[8], Francisco Ricardo Negri[9], Jonas de Souza Pereira Filho[3], Alexander Cherkinsky[10], Mário André Trindade Dantas[1,2]

[1]*Programa de Pós-graduação em Ecologia e Conservação, PPEC, Universidade Federal de Sergipe, São Cristóvão, Sergipe, Brazil. lidi.asevedo@gmail.com*

[2]*Laboratório de Ecologia e Geociências, Instituto Multidisciplinar em Saúde, Universidade Federal da Bahia, Vitória da Conquista, Bahia, Brazil.matdantas@yahoo.com.br*

[3]*Laboratório de Pesquisas Paleontológicas, Departamento de Ciências da Natureza, Universidade Federal do Acre, Rio Branco, Acre, Brazil. alceuranzi@hotmail.com, jpdesouzafilho@hotmail.com*

[4]*Department of Geography and Geology, University of Turku, Turku, Finland. riskall@utu.fi*

[5]*Department of World Cultures, University of Helsinki, Helsink, Finland. martti.parssinen@helsinki.fi*

[6]*Department of Biology, University of Turku, Turku, Finland. kalle.ruokolainen@utu.fi*

[7]*Universidade Federal de Minas Gerais, Departamento de Zoologia, Belo Horizonte, Minas Gerais, Brazil. cozzuol@icb.ufmg.br*

[8]*Museu Estadual de Rondônia, Porto Velho, Rondônia, Brazil. ednair.nascimento@gmail.com*

[9]*Laboratório de Paleontologia, Universidade Federal do Acre, Campus Floresta, Cruzeiro do Sul, Acre, Brazil. frnegri@bol.com.br*

[10] *Center for Applied Isotope Studies, University of Georgia, Atens, United States. acherkin@uga.edu*

*Corresponding author: L. Asevedo

Abstract

We report the first ^{14}C AMS datings and carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) stable isotopes data to reconstruct the paleoecology of medium to large herbivorous mammals from late Quaternary of southwestern Amazon (Acre and Rondônia states, Brazil). AMS ^{14}C datings for *Neochoerus* sp. (29,072 - 27,713 Cal yr BP), *Notiomastodon platensis* (25,454 - 24,884 Cal yr BP) and *Eremotherium laurillardi* (11,320 - 11,131 Cal yr BP) supports the Lujanian ages. All fossils have low $\delta^{13}C$ and $\delta^{18}O$ isotopic values that suggest heterogenous forest habitats, agreeing with paleovegetation reconstitution. Most species were browsers ($pi C_3$ = 100%; Niche breadth, B_A = 0), where the key species with the largest body mass, *N. platensis* (~6,300 kg) and *E. laurillardi* (~3,500 kg), possibly had a more generalized browser diet in closed-canopies to woodlands. Their diet distinguished from the C_3/C_4 generalist *Trigodonops lopesi* (~1,900 kg), which foraged in wooded savannas ($p_i C_3$ = 70%; B_A = 0.72), similarly with its relative *Toxodon platensis* (~1,800 kg) that had a browse-dominated mixed feeder diet ($p_i C_3 \geq 84\%$, $B_A \leq 0.38$) in other localities of Amazonia. *Palaeolama major* (~280 kg) was possibly a strictly folivorous within subcanopies, whereas *Tapirus* sp. (~250 kg) and *Mazama* sp. (~40 kg) were browsers in subcanopies to woodlands. *Holmesina rondoniensis* (~120 kg) was a browser but not restricted, where could also feed on herbaceous from understories in woodlands,

and *Neochoerus* sp. (~ 200 kg) feeding predominantly herbaceous plants in wooded savannas ($pi C_3$ = ~ 69%; B_A = 0.75). We estimate that the interspecific competition could have been avoid by different feeding strategies, although more investigations are still needed to better understand their ecological interactions in the habitats of the southwestern Amazon during the late Quaternary.

Keywords

Pleistocene, Amazon, megafauna, paleodiet, stable isotopes, AMS ^{14}C dating

1. Introduction

An emblematic Pleistocene fauna of herbivorous mammals is recognized in southwestern Amazon (Simpson and Paula Couto, 1981; Paula Couto, 1982, 1983a, 1983b; Ranzi, 2000; Nascimento, 2008; Ranzi, 2008). The native notoungulates, cingulates, pilosans, caviids and also the Holartic immigrants, such as proboscideans, cetartiodactyls and perissodactyls are the most significant Quaternary members in this region (Ranzi, 2000; Góis et al., 2004; Porto et al., 2004; Holanda and Cozzuol, 2006; Nascimento, 2008; Ranzi, 2008; Holanda et al., 2011).

The first fossil occurrences have been reported at the beginning of the 20th century from alluvial Quaternary deposits outcropping along the banks of the Juruá River, affluent of the Amazon River in the states of Acre and Amazonas, Brazil (Simpson and Paula Couto, 1981; Ranzi, 2000, 2008). However, the knowledge about the Pleistocene mammal fossils from Rondônia state began in the 1980s, after the beginning of intense gold mining activity in the alluvial deposits of the Madeira River, also tributary of the Amazon River (Nascimento, 2008; Holanda et al., 2011).

Despite the great faunistic diversity, there are few inferences regarding the paleoecology of these assemblages. Ranzi (2000) assessed the ecological importance of the Pleistocene fauna from Juruá River in a comparative study with modern species, although no specific method for paleocological fauna reconstruction has been performed.

The most traditional studies for paleoecological reconstructions use morphological inferences through analyses of dental hypsodonty, enamel microwear and mesowear, cranial shape adaptations, among others (e.g., Fortelius and Solounias, 2000; Solounias and Semprebon, 2002; Bargo et al., 2006; Naples and McAfee, 2012). Other studies retrieve direct evidence of the food content ingested through analysis of plant microfossils extracted from dental calculi and coprolites (e.g. Marcolino, 2012; Asevedo et al., 2012; 2020). Nevertheless, increasing number of studies are employing isotopic analysis of fossilized mammalian mineralized tissues, proving to be an excellent tool (e.g., Sánchez et al., 2004; Macfadden, 2005; Domingo et al., 2012; Lopes et al., 2013; França et al., 2014; Dantas et al., 2013; 2017; Pansani et al., 2019).

The analysis of stable isotopes in paleoecology is based on the natural variation of stable isotope composition in animals (Fricke, 2007; Koch, 2007; Higgins, 2018). Ingestion of water and food along with the physiological processes of each animal leave a geochemical impression on the inorganic (bioapatite) and organic (collagen) components of its bones and teeth (Koch, 2007). Stable isotopes of carbon in mineralized mammal tissues are derived from their food, and are closely related to the photosynthetic pathways used by the plants consumed (Fricke, 2007; Koch, 2007; Marshall et al., 2007). On the other hand, the stable isotope of oxygen is mainly derived from the water ingested by drinking and food, and accordingly brings important inferences related to climatic factors (e.g., precipitation and temperature) of the species habitats (Sponheimer and Lee-Thorp, 1999; Fricke, 2007; Koch, 2007). Therefore, the analysis of carbon and oxygen

isotopes is important to identify feeding preferences and paleoenvironment of extinct mammals, as isotopic compositions vary with diet, location and ecosystem (Fricke, 2007; Koch, 2007; Higgins, 2018).

The present study provides a reconstruction of the paleoecology of medium to large herbivorous mammal assemblages from late Quaternary of southwestern Amazon through stable carbon and oxygen isotope analyses, and also supplying: (i) ^{14}C datings by accelerator mass spectrometry (AMS) to contextualize the fossil assemblages, (ii) inferences about the paleoenvironment, and (iii) ancient diet and niche partitioning.

2. Material and methods

2.1. Samples

Eighteen bulk samples of enamel, dentin and bones were collected from species of Pilosa (Megatheriidae: *Eremotherium laurillardi* Lund, 1842), Cingulata (Pampatheriidae: *Holmesina rondoniensis* Góis et al., 2012), Proboscidea (Gomphotheriidae: *Notiomastodon platensis* Ameghino, 1888), Notoungulata (Toxodontidae*: Trigodonops lopesi* Roxo, 1921), Perissodactyla (Tapiridae: *Tapirus* sp. Brisson, 1762), Cetartiodactyla (Camelidae: *Palaeolama major* Liais, 1872 and Cervidae: *Mazama* sp. Rafinesque, 1817) and Rodentia (Caviidae: *Neochoerus* sp. Hay, 1926) (Supplementary Table 1). These samples were analyzed to obtain stable carbon and oxygen isotope composition from carbonate component of the bioapatite. AMS ^{14}C datings were performed for *E. laurillardi*, *N. platensis* and *Neochoerus* sp. samples, and were calibrated into calendar ages before present using CALIB 7.1 program (Reimer et al., 2013). Both analyses were performed at the Center for Applied Isotope Studies (CAIS) of the University of Georgia, United States.

The fossil specimens came from Quaternary alluvial deposits in several localities in the southwestern Amazon of the Upper Juruá (8°47'S - 9°49'S, 72°41'W - 72°49'W; Fig 1, locality 1, a-d) and Chandless rivers (9°49'50"S, 70°08'31"W, Fig. 1, locality 2) in Acre state, as also in Araras locality, Madeira River (10º03'01"S, 65º19'31"W; Fig. 1, locality 3), Rondônia state, Brazil. The specimens are deposited in the paleontological collections of the Laboratório de Pesquisas Paleontológicas of Universidade Federal do Acre (LPP/UFAC), Rio Branco, Acre and the Museu da Memória Rondoniense (MERO), Porto Velho, Rondônia, Brazil.

Previous data of stable carbon and oxygen isotopes of the Toxodontidae *Toxodon platensis* Owen, 1840 from southwestern Amazon in Peru (8°24'S - 12°38'S, 71°18'W - 74°17'W) and Bolivia localities (11°00'S - 14°01'S, 65°06'W - 69°00'W; Fig. 1, localities 4 - 9; Supplementary Table 1) by Macfadden (2005) were integrated into analysis in order to compare with the sympatric toxodontid *T. lopesi*, and also the other fossil taxa from Brazilian Amazonian localities.

2.2. Material processing

The stable isotope and AMS ^{14}C datings analyses followed the methodological steps of Cherkinsky (2009). Two cleaning steps were initially performed on the bone and tooth samples: first, a mechanical wash using an ultrasonic bath and wire brush to remove external material (i.e., dirt, secondary materials, etc), and second, a chemical cleaning to remove diagenetic carbon compounds. The materials were soaked overnight in 1N acetic acid, then washed free of acetic acid by repeated decantation. Loose or extraneous material was discarded and the samples were dried at approximately 70°C. After drying, samples were crushed into small fragments and again reacted with 1N acetic acid in a 250-mL Erlenmeyer flask. The flask was periodically evacuated to remove air and/or CO_2

149 from micropores, after which the flask is returned to atmospheric pressure to force fresh
150 acid into microspaces of the sample. This process of evacuation and repressuring was
151 performed at ~20-minute intervals until no substantial release of fine, foamy gas bubbles
152 occurs, and it was repeated at least 4-5 times. Once the evolution of fine gas bubbles has
153 ceased, it can be assumed that all secondary or surface-exchanged carbonates have been
154 removed.

155 The completely cleaned bone samples were washed free of acetic acid by repeated
156 soaking and decantation with demineralized water and then vacuum-dried with 100%
157 phosphoric acid to dissolve the bone/tooth mineral and release carbon dioxide from
158 hydroxyapatite. The resulting carbon dioxide was cryogenically purified from other
159 reaction products and catalytically converted to graphite. The sample ratios were
160 measured separately using a stable isotope ratio mass spectrometer.

161 All results are reported using delta notation, $\delta = [(R_{sample}/R_{standard} - 1) \times 1000]$
162 (Coplen, 1994). The reference for carbon isotope values ($R = {}^{13}C/{}^{12}C$) is Vienna Pee Dee
163 Belemnite (VPDB) and oxygen isotope ($R = {}^{18}O/{}^{16}O$) is ~~the~~ Vienna Standard Mean Ocean
164 Water (VSMOW).

165

166 2.3. Interpretation of $\delta^{13}C$ data

167 The interpretation of carbon isotope values found in tooth/bones of medium-to
168 large-bodied herbivorous mammals are based on fractionated values of the plant
169 photosynthetic pathway consumed (Fricke, 2007; Koch, 2007; Higgins, 2018). Plants
170 have two main photosynthetic pathways, C_3 and C_4 (Ehleringer and Cerling, 2002). C_3
171 plants, which fix carbon using the Calvin Cycle, comprise ~85% of terrestrial plant
172 biomass, encompassing most trees, shrubs, and grasses from high-elevation, high latitude,
173 and cool-growing seasons. The $\delta^{13}C$ values range from − 35‰ to − 22‰ with mean value

of – 27‰ (Koch, 2007; Marshall et al., 2007). Values of $\delta^{13}C$ below − 30‰ reflect C_3 plants from closed-canopy forest environments, whereas values close to the limit of C_3 plants may be associated with C_3 grasslands (e.g., − 23 to − 22‰; Kohn, 2010). C_4 plants, in turn, fix carbon using the Hatch-Slack cycle and comprise about 5-10% of the terrestrial plant biomass, including predominantly grasses, herbs and eudicotyledons adapted to arid and high luminosity index environments (Ehleringer and Cerling, 2002). The $\delta^{13}C$ values range from – 17‰ to – 9‰ and the mean value is – 13‰ (Koch, 2007; Marshall et al., 2007).

Consumers are enriched in ^{13}C compared to the plants. Previous studies demonstrated that medium-to large-bodied herbivorous mammals had an enrichment of around 14‰ (Ɛ* bioapatite-diet; Cerling and Harris, 1999). However, recently, Tejada-Lara et al. (2018) suggested that the body mass (bm) influences the physiological carbon enrichment values, and their determination should be calculated based on an equation: $Ɛ^* = 2.4 + 0.034$ (bm).

In spite of the body mass estimates for extinct species that do not have living relatives are approximations and vary in literature, it was considered the most recent published data to integrate in the analysis (i.e., Ghizzoni, 2014; Dantas, 2019; Dantas et al., 2020; Table 1). For the fossils of extant taxa, *Tapirus* sp. and *Mazama* sp., we followed the body mass data of the most common species of the respective genera in the Amazon region, *Tapirus terrestris* Linnaeus, 1758 (i.e., Padilla and Dowler, 1994) and *Mazama americana* Erxleben, 1777 (i.e., Duarte and Jorge, 1996; Table 1). Through these data, it was calculated an enrichment of 12‰ for taxon with body mass less than 75 kg, 13‰ for those species between 75 kg to 600 kg, 14‰ between 600 kg to 3,500 kg, and 15‰ for species as from 3,500 kg.

198 Accordingly, diet categories based on the digestive physiology of herbivores can be
199 discerned between browsers, grazers and mixed feeders. Browser mammals consume
200 larger proportions of fruit and foliage from C_3 shrub and tree plants (Fricke, 2007; Koch,
201 2007; Higgins, 2018), and based on the different enrichments in bioapatite (i.e., 15‰ to
202 12‰), they have average $\delta^{13}C$ values of – 12‰ to – 15‰, respectively. Grazing mammals
203 are consumers of herbs and grasses (Fricke, 2007; Koch, 2007; Higgins, 2018). C_3 grazers
204 may have $\delta^{13}C$ values approximately between – 8‰ to – 7‰ and – 11‰ to – 10‰,
205 although it is still difficult to distinguish the diet between C_3 grasses and wood resources,
206 due to the overlap in $\delta^{13}C$ values for certain phytophysiognomies (e.g., C_3 grassland and
207 wooded savanna). On the other hand, C_4 grazers have specific average $\delta^{13}C$ values of 2‰
208 to –1‰. Mixed feeder species that consume both browse and grass (C_3-C_4), have
209 intermediate values between the average of browsers and C_4 grazers (– 12‰ to – 15‰
210 and 2‰ to –1‰).
211 In order to identify the landscape characteristics of mammalian fossil habitats, we
212 used the interpretation of the $\delta^{13}C$ ranges from Domingo et al. (2012) following the
213 specific enrichment values. Therefore, species from (i) closed-canopy forest habitats [i.e.,
214 higher density areas of trees forming canopy] have values from – 20‰ and – 15‰ to –
215 23‰ and – 18‰; (ii) mesic woodland habitats [i.e., low-density forest with sparse
216 understory plants] have values from – 15‰ and – 10‰ to – 18‰ and – 13‰; (iii) wooded
217 C_3 grassland [i.e., arboreal savannas] have values from – 10‰ and – 7‰ to – 13‰ and –
218 10‰; (iv) mixed C_3 and C_4 habitats [i.e., arboreal savannas] have values from – 7‰ and
219 – 2‰ to – 10‰ and – 5‰; and (iv) open C_4 grassland habitats [i.e., open savannas] have
220 values from – 2‰ and 6‰ to – 5‰ and 3‰.
221 Comparisons between carbon isotope values of the fossil taxa and the living related
222 species from the literature were performed taking into account the enrichment addition of

223 2‰ to the extant species, because of the $\delta^{13}C$ decay of atmospheric CO_2 in current
224 ecosystems (Suess effect), as a consequence of the large burning of fossil fuels since the
225 beginning of the Industrial Revolution in the 18th century (Keeling, 1979). Previous data
226 of stable carbon isotopes analyzed in collagen samples from current species were
227 converted to bioapatite values. Herbivorous mammal collagen is known to be 5‰
228 enriched in relation to the food (Koch, 2007). Thus, following Tejada-Lara (2018), from
229 the $\delta^{13}C$ value of the resource found ($\delta^{13}C_{collagen}$ – 5‰) was added the specific enrichment
230 values for bioapatite according to the body mass of the species.
231
232 2.3.1. Diet proportions and ecological niches estimates
233 In order to refine the diet interpretations, the $\delta^{13}C$ data and respective enrichment
234 values considered for each taxon were used to calculate the proportion of C_3 and C_4 diet
235 for the species, using the following equation presented by Phillips (2012):

236 $$(1) \quad \delta^{13}C_{mix} = \delta^{13}C_1 f_1 + \delta^{13}C_2 f_2$$

237 $$(2) \quad 1 = f_1 + f_2$$

238 Where, **C** represents the mean $\delta^{13}C$ values of C_3 (C_1= –12‰ to –15‰) and C_4
239 (C_2 =2‰ to –1‰) plant consumers. $\boldsymbol{f_1}$and $\boldsymbol{f_2}$ are the proportion of C_3 and C_4 resources,
240 respectively.
241 Through the values obtained from the proportion of resources it was possible to
242 calculate the ecological niche breadth according to the following Pianka (1973)
243 equation:

244 $$B = 1/\sum p_i^2$$

245 Where, $\boldsymbol{B}$ is the niche breadth and $\boldsymbol{p_i}$ the proportion of resources consumed.
246 This measure was then standardized from 0 to 1 following the equation of Levins (1968):

247 $$B_A = B - 1/n - 1$$

Where, $\boldsymbol{B_A}$ is standardized niche width, B is the niche breadth, and **n** is the number of resources consumed. The results indicate whether the animal is specialist (0) or generalist (1)

2.4. Interpretation of $\delta^{18}O$ data

The stable isotope of oxygen in mammalian bioapatite is directly related to their body water. It reflects the oxygen isotope composition that enters in organism through atmospheric O_2, ingested water and food sources, and exits via respiration, transpiration and excretion. Thereby, resulting in a complex function of climate, diet and physiology (Sponheimer and Lee-Thorp, 1999; Koch, 2007).

Since the $\delta^{18}O$ values of atmospheric O_2 are relatively constant, large herbivorous mammals that require considerable amount of ingested water from lakers and rivers, have $\delta^{18}O$ values reflecting the response of meteoric water ($\delta^{18}O_{mw}$) to changes in temperature and/or precipitation/humidity (Sponheimer and Lee-Thorp, 1999; Fricke, 2007; Koch, 2007), which can be influenced geographically and temporally by several climatic factors (e.g., continentality, latitude, altitude, amount effect, among others; Sponheimer and Lee-Thorp, 1999; MacFadden and Higgins 2004; Koch, 2007; Higgins, 2018).

Traditionally, in terrestrial ecosystems the more positive $\delta^{18}O$ values in mammal tissues are indicative of warmer and/or drier habitats/seasons, due to the ^{18}O-enrichment in detriment of the higher ^{16}O-evapotranspiration in ingested waters and plants (Sponheimer and Lee-Thorp, 1999; Fricke, 2007; Koch, 2007). The evapotranspiration effect is larger in C_4 plants that do not close their stomata, and consequently grazer mammals have the most enriched $\delta^{18}O$ values (Fricke, 2007; Koch, 2007). On the other hand, negative $\delta^{18}O$ values may reflect a colder and/or wetter habitats/seasons, which contributes to depletion of ^{18}O from water surfaces and plants (Sponheimer and Lee-

Thorp, 1999; Fricke, 2007; Koch, 2007). Specifically, in tropical forested habitats, the reduction of ^{16}O evapotranspiration in C_3 plants adapted to shaded environments, plus the amount effect that cause a depression in the oxygen isotopic curves related to the high precipitation may favors the depletion in $\delta^{18}O$ values for browser mammals (MacFadden and Higgins 2004; Fricke, 2007; Koch, 2007; Higgins, 2018).

Mammal species inhabiting similar environments can also vary their $\delta^{18}O$ data in response to different proportion of drinking water surfaces as opposed to plant water consumptions (Sponheimer and Lee-Thorp, 1999; Levin et al., 2006). Some herbivorous mammals get most of their water from plants, and have the $\delta^{18}O$ values reflecting not only the local precipitation, but also the local environmental relative humidity that control the ^{18}O enrichment in plants (Ayliffe et al., 1992). These taxa are sensitive to changes in $\delta^{18}O$ values with increased aridity (evaporation-sensitive), differing to those taxa that are obligatory drinkers (evaporation-insensitive; Levin et al., 2006).

2.4.1. Estimation of $\delta^{18}O$ in ancient environmental waters

The oxygen values in bioapatite of obligatory drinkers can be used as a proxy to past meteoric water $\delta^{18}O$ estimation. Such relationship is consistent with the relationship between measured phosphate $\delta^{18}O$ values (^{18}Op) of bones and teeth of modern African (*Loxodonta africana* Blumenbach, 1797) and Asian (*Elephas maximus* Linnaeus, 1758) elephants and estimates of $^{18}O_{mw}$ (Ayliffe et al., 1992). Thus, assuming modern elephants are a reasonable analog for the South American proboscidean *N. platensis*, we converted its isotopic values from bioapatite carbonate ($\delta^{18}Oc$) to phosphate values ($\delta^{18}Op$) by reducing the $\delta^{18}Oc$ values to 8.7‰ (Bryant et al., 1996). Posteriorly, it was calculated the $\delta^{18}O_{mw}$ of *N. platensis* using the relationship between the oxygen content of the PO_4

297 component of bioapatite ($\delta^{18}Op$) and ingested water in modern elephants through the
298 equation of Ayliffe et al. (1992):

299 $$\delta^{18}Op = 0.94\delta^{18}O_{mw} + 23.3$$

300

301 **3. Results**

302 The ^{14}C AMS datings indicate that the specimens are biostratigraphically correlated
303 to the Lujanian Stage/Age (SALMA), and include similar ages for *Neochoerus* sp.
304 (29,072 - 27,713 cal yr BP) and *N. platensis* (25,454 - 24,884 cal yr BP) from Madeira
305 and Juruá rivers in Rondônia and Acre states, respectively. Furthermore, a more recent
306 age was obtained for *E. laurillardi* (11,320 - 11,131 cal yr BP) from the Chandless River,
307 Acre state (Supplementary Table 1).

308 The low $\delta^{13}C$ values obtained from bioapatite in mammals from the southwestern
309 Amazon Pleistocene mammals (– 17.47‰ to – 8.83‰; Supplementary Table 1), indicate
310 a tendency toward a C_3 specialist diet ($p_iC_3 = 100\%$; $B_A = 0$) from closed-canopy forest
311 to wooded C_3 grasslands (Table 1; Fig. 2).

312 The largest bodied species *N. platensis* (bm: ~ 6,300 kg) and *E. laurillardi* (bm: ~
313 3,500 kg) have $\delta^{13}C$ values below the average of – 12 ‰ for C_3 diet, which indicate
314 browsing diet in more closed physiognomies (Fig. 2A). *E. laurillardi* possibly inhabited
315 closed-canopy forests in Acre (Juruá River: – 17.04 ± 0.20 ‰; Chandlers River: – 15.37
316 ‰) and mesic woodlands in Rondônia (–14.23‰; Table 1). *N. platensis*, in turn, has a
317 slightly broad range of $\delta^{13}C$ values and inhabited closed-canopy forests and mesic
318 woodlands in both localities of Acre (– 14.11 ± 2.4 ‰) and Rondônia (– 15.09 ± 1.16 ‰;
319 Table 1; Fig. 2A).

320 Among the species with the highest body mass, the notoungulate *T. lopesi* (bm: ~
321 1,900 kg) of Rondônia has a $\delta^{13}C$ value significantly more positive (– 8.83 ‰; Table 1),

indicative of mixed feeder (B_A = 0.72) in wooded savanna-like habitats with dominant C_3 plants (p_iC_3 = 70 %; Table 1; Fig. 2B). For the sympatric toxodontid *T. platensis* (bm: ~ 1,800 kg) from southwestern Amazon localities in Bolivia (– 13.9 ± 1.6‰; $p_i C_3 \geq 86\%$, $B_A \leq 0.32$) and Peru (– 13.2± 1.4 ‰; $p_iC_3 \geq 84\%$, $B_A \leq 0.38$) by Macfadden (2005), the $\delta^{13}C$ values indicate browse-dominated mixed feeder habits in mesic woodlands to wooded C_3 grasslands (Table 1; Fig. 2B).

For the mammal species with lower body mass, a more positive $\delta^{13}C$ value was observed for the large capybara *Neochoerus* sp. (bm: ~ 200 kg) from Rondônia (– 9.66 ‰) close to the value found in the toxodont for the same region (Fig. 2). The species probably had a more generalist diet between C_3 and C_4 resources (B_A = 0.75), accessing more open landscapes dominated by C_3 plants ($p_i C_3$ = 69 %; Table 1; Fig. 2C).

The other mammal species have $\delta^{13}C$ values below the average of –14 ‰ and –15 ‰ (Ɛ* =13 and 12 ‰, respectively), and also pointed to specialist browser diet such as the ground sloth and the proboscidean (Fig. 2C). *Tapirus* sp. (bm: ~ 250 kg) probably was a browser in closed-canopy forests in Juruá River (– 17.33 ‰) and mesic woodlands in Rondônia (– 14.77 ‰; Table 1; Fig. 2C). The camelid *P. major* (bm: ~ 280 kg) was a browser in closed-canopy forest in Juruá River (–17.47 ‰), and the pampatheriid *H. rondoniensis* (bm:~ 120 kg) and the cervid *Mazama* sp. (bm: ~ 40kg) were browsers in ~~solely~~ mesic woodlands habitats in Rondônia (– 14.89 ‰ and – 15.47 ‰, respectively; Table 1; Fig. 2C).

The $\delta^{18}O$ values are constantly low for all the species (19.90 to 25.80 ‰; Table 1; Supplementary Table 1; Fig. 2), indicating similar conditions in precipitation amount and degree of rainfall/transpiration for both forest and wooded savanna landscapes in localities of Acre and Rondônia states. The slightly $\delta^{18}O$ variations may have been influenced by monsoonal climates (wet and dry seasons) affecting the $\delta^{18}O$ values of

347 ingested water ($\delta^{18}O_{mw}$). The $\delta^{18}O_{mw}$ results for *N. platensis* point more ^{18}O-depleted
348 water sources around the Madeira River in Rondônia (mean = – 9.50‰ ± 0.9‰) compared
349 to the localities of Juruá River in Acre (mean = – 7.51‰ ± 0.5‰; Table 2). It corroborates
350 with the lowest $\delta^{18}O$ values founded for the generalists *T. lopesi* and *Neochoerus* sp. also
351 from Rondônia (20.29 ‰ and 19.90 ‰; Table 1; Fig. 2B and C). Their oxygen results
352 plus the enriched $\delta^{13}C$ values can indicate a more open habitats close to riverine resources.
353 By contrast, the browser *P. major* from Acre, showed the highest $\delta^{18}O$ value (25.80 ‰;
354 Table 1; Fig. 2C), probably related to the consumption of more ^{18}O-enriched water
355 sources. Although, the more depleted $\delta^{13}C$ values found in this camelid may also indicate
356 a significant diet of foliage, and would explain the more positive oxygen value, because
357 leaf water is more ^{18}O-enriched.
358
359 **4. Discussion**
360 *4.1. Radiocarbon dating of mammal assemblages from southwestern Amazon*
361 The AMS ^{14}C datings of the fossils indicate that the mammal assemblages from
362 southwestern Amazon in Acre and Rondônia states are biostratigraphically correlated to
363 the Lujanian Stage/Age SALMA. Late Pleistocene ages were obtained for Juruá and
364 Madeira river records, which is in agreement to the chronological and biostratigraphy of
365 fossiliferous deposits for both rivers (~ 43 to 29 ka BP and ~ > 46 to 27 Ka BP,
366 respectively; Latrubesse and Rancy, 1998; Rizzotto and Oliveira, 2005), whereas an early
367 Holocene age was obtained for the new record in Chandless River, Acre.
368 The Pleistocene assemblages are also chronologically correlated to the fossil
369 records of other river basins of western Amazonia, including the Ucayali River, Peru (40
370 to 32 ka BP), Madre de Dios River, Peru (38 to 36 ka BP), and Caquetá River, Colombia
371 (55 to 30 Ka BP; Latrubesse and Rancy, 1998).

372

373 *4.2. The habitat landscapes from late Quaternary of southwestern Amazon*

374 The isotopic carbon and oxygen signature of the late Quaternary mammals from
375 Acre and Rondônia states, support that the paleocommunity would have inhabited C_3-
376 dominated environments, with species occurring from closed-canopies, mesic woodlands
377 to wooded savannas (Fig. 3A-C). The suggested environmental heterogeneity also
378 characterizes the modern landscapes of the southwestern Amazon, consisting of non-
379 flooded "Terra Firme" and periodically flooded Várzea forests.~~,~~ T~~t~~he dominant regional
380 physiognomy is composed of spaced trees with few dense shrubby strata (open
381 ombrophilous forest), with floristic formations also composed of palm trees (e.g., *Attalea*
382 *speciosa*), bamboos (e.g., *Guadua superba*) and sororocas (e.g., *Phenakospermum*
383 *guianensis*). Closed canopy forests (dense ombrophilous forests) to open ones
384 conditioned by climate seasonality (semideciduous seasonal forests), mixed forest and
385 grassy-woody vegetation (campinaranas), and forested savannas also configure the
386 current physioecological zones of this rich Amazon region (IBGE, 2012).

387 The paleoenvironmental interpretation of the late Quaternary in Amazonia is an
388 issue still debated. Many paleoenvironmental reconstructions suggest that the distribution
389 of the Amazonian rainforest has changed mainly due to climatic fluctuations during
390 glacial/interglacial events. As consequence, it was proposed alternating periods of forest
391 contraction forming refuge regions followed by its expansion during distinct dry and wet
392 conditions (Haffer, 1969; Liu and Colinvaux, 1985; Bush et al., 1990; Colinvaux et al.,
393 1996; Ledru, 2002; Ledru et al., 2006), savanna corridors during Last Glaciation (van der
394 Hammen and Hooghiemstra, 2000), as well as retractions of equatorial rain forests
395 associate to expansion of tropical ones (similar to Atlantic forest; Arruda et al., 2017).
396 Nevertheless, some studies do not support these changes in landscapes, and suggest a

paleoclimatic scenario relatively undisturbed for Amazonian rainforest during the last 50 ka BP (Colinvaux et al., 1996, 2000, 2001; Bush et al., 2004; Irion et al., 2006; Mayle and Power, 2008).

The isotopic results of the mammalian fossils do not correspond with abrupt changes in the C_3 landscapes. The carbon and oxygen isotope values persist constantly low for all the specimens analyzed, including fossils of the glacial periods around ~ 30 to 25 ka BP (^{14}C results of *Neochoerus* sp and *N. platensis*, respectively), and of the beginning in interglacial period around ~11 ka BP (^{14}C dating of *E. laurillardi*). These data are in concordance with the isotope data of *T. platensis* specimens from Amazonian localities in Peru and Bolivia with ages ranging from ~ 38 ka to 15 ka BP evaluated by Macfadden (2005).

These results corroborate with the humid climate conditions during the late glacial - early Holocene estimated for the southwestern Amazon. Specifically, in Rondônia state, palynological analysis indicate that forests were dominant in Katira creek around 55 ka to 26 ka BP (van der Hammen and Absy, 1994) and in Madeira Formation during 46 to 27 ka BP (Rizzotto and Oliveira, 2005). Through isotopic, sedimentological and geomorphological analyses performed in a marginal area of Madeira river, Rossetti et al. (2017) also confirmed that the climate was wet and cold from 40 ka BP up to the Last Glaciation Maximum (LGM). Pollen data indicates the presence of cold-adapted plants (e.g., *Alnus*, *Hedyosmum*, *Weinmannia* and *Podocarpus*), which became absent in the Holocene, in association with herbs and tree taxa similar to modern ones (Cohen et al. 2014).

During the LGM, the humidity was reduced and the temperature was between 2° and 6°C below modern values (van der Hammen and Absy 1994; van der Hammen and Hooghiemstra 2000; Cohen et al. 2014). Thus, an intensified aridity toward the end of the

late Pleistocene was estimated in Madeira river region (Rossetti et al., 2017), whereas savanna expansion was proposed for Katira site related to a dry climatic phase between 26 to 13 ka BP (van der Hammen and Absy, 1994). On the other hand, in localities of Amazonas and Rondônia border, the carbon isotopes of soil organic matter suggest that these regions were still covered by forest vegetation between17 to 9 ka BP (Freitas et al., 2001).

In spite of the carbon isotope results of *T. lopesi* and *Neochoerus* sp. from Rondônia indicating foraging in habitats with low proportion of C_4 plants (~30%), the isotopic signature consistently low for the most of the analyzed specimens do not support dominance of savanna habitats as previously inferred for the same assemblages in other studies (Latrubesse and Rancy, 1998; Ranzi, 2000; Ranzi, 2008). Ground sloths, proboscideans, toxodonts and cingulates were animals able to feed~~ing~~ on grasses, thus if the dry savanna habitats were present in southwestern Amazon, the carbon isotope values characteristic of C_4 plants would have been more significant. On the other hand, our data indicate that some species possibly were inhabiting closed canopy forests and consumed plants with carbon values below – 30‰. These values are seen in plants that are under the influence of the "canopy effect", which produces ^{13}C-depleted and a gradient of leaf $\delta^{13}C$ values from the ground (most negative values) to the canopy (van der Merwe and Medina, 1991).

Furthermore, an interesting fossil record of *Guadua* sp. in Madre de Dios (Peru), which currently makes up extensive areas of bamboo forests in southwestern Amazonia, suggests that these forests were already present prior to the LGM (~ 3.12 ± 0.02 Ma and ~45 ka BP; Olivier et al., 2009), and that Pleistocene mammals could also have been accessed.

The depleted $\delta^{18}O_{mw}$ of *N. platensis* reflects to the "continental and amount effects" that occurs in tropical amazon. Thus, it seems consistent with speleothem and stalagmite oxygen isotope data from western Amazonia. For Cueva Santiago in Amazonian Ecuador the results do not indicate prolonged drying during the last 95 ka ($\delta^{18}O$ = – 8.05 to – 4.52 ‰), and the climate condition during the LGM (23 ka and 19 ka BP) was wetter (Mosblech et al., 2012). Similarly, in El Condor and Cueva del Diamante caves, both located on the eastern flank of the Andes in northern Peru, indicate a wetter LGM and a drier early-mid Holocene in an opposite pattern to eastern Amazon (Cheng et al., 2013).

Based on oxygen isotopes in fluid inclusions from speleothems from Cueva del Tigre Perdido, in Peruvian Amazon, van Breukelen et al. (2008) proposed that the temperature change was small throughout the last ~13.5 ka BP, but the rainfall amount was reduced by 15–30% below present values. Thus, according to carbon isotopes of soil analysis the warmer and drier conditions could support savanna vegetation in Rondônia only during the early to middle Holocene, whereas during the late Holocene the moisture favored the expansion of the Amazonian rainforest as known today (Pessenda et al., 1998; Freitas et al.,2001). By contrast, any major shift of the forest vegetation toward open savanna was notified for the last 10 ka in the eastern Acre at Severino Calazans (Parssinen et al., in press).

~~*4.1.*~~*4.3. Feeding ecology of the late Pleistocene mammals*

In the ancient assemblages of Amazon Quaternary mammals, most species were browsers feeding mostly on leaves and fruits of arboreal/scrub plants. The largest bodied species, *E. laurillardi* and *N. platensis*, probably occupied similar niches in southwestern Amazon, inhabiting from closed-canopy forests to mesic woodlands. The slightly wider range of carbon values for the proboscideans indicates a greater food plasticity (Fig. 4A

and B; Supplementary Table 1). *N. platensis* was an endemic proboscidean from South America, whose generalist diet was probably similar to the extant elephants. Diet followed habitat phytophysiognomy, and it consisted predominantly of herbaceous plants, foliar and floral branches, fruits and woody parts (Asevedo et al., 2012; 2020; Mothé et al., 2017). According to the carbon isotopes data, this proboscidean could have been a specialist C_3 browser in forest habitats of southwestern Amazon ($\mu\delta^{13}C$ = – 15.39 ± 1.63 ‰; median: -15.61; IQR: -2.21; Fig. 4B), but was a browser or mixed feeder in C_3 woodlands/grasslands from Pampean regions of Argentina, Uruguay and Brazil ($\mu\delta^{13}C$ = – 8.2 ± 2.1 ‰; median: -8.26; IQR: -1.4; Fig. 4B; Sánchez et al., 2004; Gutiérrez et al., 2005; Domingo et al., 2012; Lopes et al., 2013), a dominant grazing diet in C_4 grasslands in the Brazilian Intertropical Region (BIR; $\mu\delta^{13}C$ = – 1.08 ± 2.66 ‰; median: -0.20; IQR: -1.78; Fig. 4B;Sánchez et al., 2004; Viana et al., 2011; Dantas et al., 2013; França et al., 2014; Dantas et al., 2017; Pansani et al., 2019), and a mixed feeding diet in C_3-C_4 woodland/grassland landscapes in Andean regions of Ecuador and Peru ($\mu\delta^{13}C$ = – 4.7 ± 3.11 ‰; median: -5.72; IQR: -6.45; Fig. 4B; Sánchez et al., 2004; Domingo et al., 2012), and also in Argentinean Chaco ($\mu\delta^{13}C$ = – 4.8 ± 3.27 ‰; median: -4.63; IQR: -5.58; Fig. 4B; Alberdi et al., 2008; Domingo et al., 2012).

With a Pan-American distribution covering the southeastern North America to southern Brazil, the ground sloth *E. laurillardi* has also been estimated as a generalist species (Dantas et al., 2017). The carbon isotope analysis in specimens of the BIR demonstrated a large range that covers pure C_3 (browser), mixed feeders and pure C_4 (grazer) consumers ($\mu\delta^{13}C$ = – 5.4 ± 3.92 ‰; median: -5.11; IQR: -4.54; Fig. 4A; Viana et al., 2011; Dantas et al., 2013, 2014; França et al., 2014; Dantas et al., 2017; Pansani et al., 2019), differing from our results for an exclusive C_3 browser pattern in the Brazilian Amazon ($\mu\delta^{13}C$ = – 15.92 ± 1.38 ‰; median: -16.14; IQR: -2.60; Fig. 4A).

The reconstruction of the cranial musculature of *E. laurillardi* by Naples and McAfee (2012) suggested a masticatory pattern that could increase in efficiency for each chewing cycle. The high ability of oral processing related to the low digestive efficiency was suggested for the other American giant sloth species, *Megatherium Americanum* (Bargo et al., 2006). This species that had a similar biomechanical apparatus compared to *E. laurillardi*, probably was a generalized selective feeder, capable of consuming a variety of turgid or moderate to soft tough and abrasive food items (Oliveira et al., 2020). *E. laurillardi* would be able to browse on small branches, leaves, and fruits and possibly had a more selective diet in Amazonian localities than *N. platensis*.

On the other hand, the toxodonts, especially *T. lopesi*, have the highest ecological niche breadth among the megamammal species from Amazon, suggesting a more generalist diet between C_3/C_4 resources, tough in C_3 dominant-landscapes. These animals were native ungulates from Pleistocene of South America with very high-crowned teeth (hypselodont), presumably used for grazing abrasive plants (Bond et al., 1997). The isotopic data for *T. platensis*, whose paleoecological interpretations are more complete, have indicated capacity to feed on a variety of vegetation (Macfadden, 2005). *T. platensis* possibly had a predominant diet composed by foliage and fruit of wood plants in southwestern Amazon localities ($\mu\delta^{13}C$ = – 13.39 ± 1.49 ‰; median: -13; IQR: -2.35; Fig. 4C; Macfadden, 2005), different than individuals from the BIR that had a wide food spectrum, ranging from browsers to grazers on C_3 plants and mixed C_3-C_4 diets in woodlands and grasslands, and also in open C_4–dominated grasslands habitats ($\mu\delta^{13}C$ = – 5.08 ± 5.76 ‰; median: -4.22; IQR: -10.81; Fig. 4C; Macfadden, 2005; Viana et al., 2011; Dantas et al., 2013; França et al., 2014; Dantas et al., 2017; Pansani et al., 2019). *T. platensis* from Argentinean and Brazilian Pampa also had mixed C_3/C_4 diets ($\mu\delta^{13}C$ = – 6.03 ± 2.66 ‰; median: -5.15; IQR: -3.28; Fig. 4C; Macfadden, 2005; Lopes et al.,

2013), whereas the individuals from the Bolivian and Argentinean Chaco had a more specialized grazer diet in C_4-dominated open grasslands ($\mu\delta^{13}C$ = 0.38 ± 1.21 ‰; median: -0.40; IQR: -2; Fig. 4C; Macfadden, 2005).

Unfortunately, there are no other paleoecological inferences for *T. lopesi* that would facilitate the understanding of its feeding behavior. This species had an intertropical distribution in northern, northeastern and southeastern Brazil and could have coexisted with *T. platensis*, who was widely distributed in South America (Mendonça, 2012). The less negative value of carbon isotope from *T. lopesi* suggests a more generalist diet compared to *T. platensis*. However, this only result is insufficient to presuppose distinction between their ecological niches, thus more investigations are needed.

Regarding large and medium-sized species, the extinc~~an~~t capybara *Neochoerus* sp. has the highest ecological niche breadth. It presented carbon and oxygen isotope values very similar to the sympatric *T. lopesi* from Rondônia region (Table 1), indicating a more C_3-C_4 generalist diet in wooded savanna habitats closely of ^{18}O-depleted water sources (Fig. 3C). The current capybara *Hydrochoerus hydrochaeris* Linnaeus, 1766 has semiaquatic habit and are native to wetlands in South America. This rodent are folivores and consumes protein-rich plants near water bodies, particularly grasses and sedges (Corriale and Loponte, 2015). The carbon stable isotopes from dental bioapatite of specimens from Amazonian Peru indicate a C_4 diet ($\mu\delta^{13}C$ = -1.6 ± 3.4‰; Tejada-Lara et al., 2020), whereas the species in Corrientes province, Argentina, consume predominantly C_3 grasses and sedges ($\mu\delta^{13}C_{\text{collagen}} = -15.7 \pm 0.3$ ‰; $\delta^{13}C_{\text{bioapatite}} = \sim -6$ ‰; Corriale and Loponte, 2015). Thus, based on feeding behavior of living capybaras we presumed that a significant portion of the Pleistocene capybara diet was also composed of herbaceous plants.

The camelid *P. major* probably had a more selective browser diet ~~for the consumption~~ of dicot foliage plants, due to the very negative $\delta^{13}C$ values. Leaves are more depleted in~~at~~ ^{13}C than other vegetative structures such as roots, stems and fruits (Badeck et al., 2005). In addition, this specimen presented $\delta^{18}O$ value more positive than other taxa that could be associated to ingestion of more ^{18}O-enriched water sources, but could also be the reflection of a folivore diet, since leaf water is more ^{18}O-enriched than meteoric water (Sponheimer and Lee-Torp, 1999). The oxygen isotope aridity index for several Pleistocene taxa from southeastern and southwestern United States developed by Yann et al. (2013), discriminates the camelids (i.e., *Palaeolama* and *Hemiauchenia*) with the greatest mean aridity index followed by antilocaprids and cervids. This supports the argument that most $\delta^{18}O$ values of those taxa comes from the water in food ingested instead the meteoric water, thus corroborating with the folivore diet inference for the camelid from southwestern Amazon.

The identification of leaves and branches of shrub angiosperms fossil remains in *P. major* coprolites from BIR in Bahia state strengthens the inference of a browser diet (Marcolino et al., 2012). Stable isotope data from that region indicates significant consumption of C_3 plants ($\delta^{13}C = -7.34$ ‰; Dantas et al., 2020), therefore in a predominantly open landscape the species probably could inhabit forest edges (Marcolino et al., 2012). Accordingly, browser habits could be a predominant behavior for this camelid.

For the fossils of extant taxa, *Tapirus* sp. and *Mazama* sp., the fruit consumption could be more abundant than for the *P. major* in late Pleistocene. The lowland tapir *Tapirus terrestris* is the largest terrestrial mammal in South America, which occurs from Colombia to northern Argentina in a wide range of ecosystems, including tropical moist forest, xeric Chaco and Cerrado forest, savanna wetlands, and lower montane forest

570 (Bodmer, 1990b). *T. terrestris* has a primarily browsing diet, and when the fruits are
571 available may consume extensively (Bodmer, 1990b). Thus, the tapir plays a key role in
572 dispersing seeds, especially large ones, for over longer distances, due to their large home
573 range, varying from 220 to 470 ha (Fragoso et al., 2000, 2003). Similar to our results, the
574 isotopic data of carbon of extant *T. terrestris* in locaties of Brazil, Colombia, Venezuela,
575 Peru and Bolivia shows low values associated with high proportion of wood plants
576 consumption ($\mu\delta^{13}C = -13.6 \pm 1.6$ ‰; DeSantis, 2011).

577 The red brocket deer *Mazama americana* is one of the most abundant and widely
578 distributed cervids in Neotropical forests (Redford and Eisenberg, 1992; Eisenberg and
579 Redford, 1999). Its distribution area ranges from Colombia and Venezuela to northern
580 Argentina and southern Brazil, and also occur in a variety of ecosystems such as montane
581 forests, lowland dry forest, rainforests and savannas located near forest edges (Emmons
582 and Feer, 1997). Feeding ecology data from Amazonian populations indicate a fruit and
583 seed-eating diet, whereas leaves, flowers and fungi are also consumed in less quantity
584 (Branan et al., 1985; Bodmer, 1990a, Gayot et al., 2004). A seasonal change in feeding
585 habits was observed by Branan et al. (1985) in Surinam forests, where diet became
586 folivorous due to fruit scarcity during dry season. Geographic differences in the diet can
587 be observed comparing studies made in French Guyana (Gayot et al., 2004) and in the
588 Peruvian Amazon (Bodmer, 1990a), where the proportions of fruit in diet were 56 % and
589 81 %, respectively.

590 In the Parque Estadual Chandless (PEC), Acre state, *T. terrestris* and *M. americana*
591 co-occur in a mosaic of heterogeneous forest landscapes, where flood pulses and the
592 presence of open forests subject to the dynamics exerted by the presence of bamboo form
593 a complex of successional gradients (Borges, 2014). *T. terrestris* occurs predominantly
594 in patches of forests near rivers or forest creeks (igarapés) with a predominance of small

595 branches of pioneer plant species and succulent shoots, sometimes it was observed
596 consuming stems and leaves of young individuals of *Cecropia* sp. and other pioneer
597 species. *M. americana*, in turn, apparently avoided denser forests and opted for more open
598 areas. Bodmer (1990) working with large ungulates in the Ucayaly River region, Peru,
599 found that *M. americana* tends to avoid floodplains, although this pattern was not clearly
600 noted in the PEC (Borges, 2014).

601 The carbon isotope composition of modern *T. terrestris* and *M. americana* from
602 Madre de Dios in Peruvian Amazon ($\mu\delta^{13}C = -14.6‰ \pm 0.6$ ‰ and -13.1 ± 1.1 ‰,
603 respectively; Tejada-Lara et al., 2020), and the carbon isotope composition in collagen
604 from Venezuelan Amazon ($\delta^{13}C_{collagen} = -23.5‰$; $\delta^{13}C_{bioapatite} = -15.5$ ‰ and -21.7 ‰;
605 -14.7 ‰, respectively; van der Merwe and Medina, 1991) did not diagnose very
606 significant differences, although the slight difference was attributed to different dietary
607 compositions between leaves and fruits. These values are similar to our data for the late
608 Pleistocene, *T. terrestris* ($\mu\delta^{13}C = -16.05$ ‰) with more negative values associated with
609 a greater preference for more enclosed environments than *Mazama* sp. ($\delta^{13}C = -15.47$
610 ‰). Thus, we infer that with similar strategies to the present, these ungulates would have
611 different foraging strategies, varying spatially and even seasonally in order to avoid
612 interspecific competitions.

613 Finally, the isotope value of carbon suggests a browsing diet for the pampatheriid
614 *H. rondoniensis* that inhabited mesic woodlands habitats in the Rondônia region, and
615 contrasts with the dominant grazing habit for the genus suggested by morphological
616 analysis of teeth and mandibular apparatus (Vizcaíno et al., 1998). Despite the efficiency
617 in consuming more abrasive vegetation, the previous inference supports that the taxon
618 was not a strictly grazer. A mixed C_3-C_4 diet of woody and grassy plants was suggested
619 by stable isotope analysis for *H. paulacoutoi* species that inhabited the BIR during the

late Pleistocene ($\delta^{13}C = -6.05$ ‰; Dantas et al., 2020), indicating that these cingulates could also have a more generalist diet. *Holmesina* is associated with wetter and warmer climate environments when compared to the pampatheriid *Pampatherium* from arid and cold environments (Vizcaíno et al., 1998; De Iuliis et al., 2001; Scillato-Yané et al., 2005), and may corresponds with the occurrence in more forested landscapes in southwestern Amazonia. It is possible that the analyzed individual of *H. rondoniensis* was foraging on the understory vegetation, feeding predominantly on foliage and fruits of tree/shrub plants, although herbaceous plants were also potentially consumed by these animals.

~~4.2.~~4.4. *Niche partitioning strategies and ecological roles from the late Pleistocene mammal assemblages*

In terrestrial ecosystems composed by assemblages of large mammals, the megaherbivores (≥1,000 kg) are considered ecological engineers capable of altering vegetation on a landscape scale. With large body size they may disrupt ecosystem structure by directly destroying woody vegetation and consuming large amounts of foliage, and therefore they are generally considered to be limited from the "bottom-up" by food availability, tough exert strong "top-down" control on vegetation structure and composition (Owen-Smith, 1992).

The modern elephant *Loxodonta africana* Blumenbach, 1797 is considered a key species structuring savanna ecosystems. It acts in the modeling of the environment, facilitating the access to resources by other middle-sized species, and limiting the abundance of other megamammal species through the competition for resources (Fritz et al., 2002).

With an ecological role similar to extant elephants, we presuppose that the species with the largest body mass, *N. platensis* (6,300 kg) and *E. laurillardi* (3,500 kg), were

probably the key species that~~which~~ structured mammal assemblages in the southwestern Amazon during the late Pleistocene. Both species were potentially competitors, although the great plasticity and foraging ability of the proboscideans could contribute for a larger home range and possibility to access different resources. The toxodonts *T. lopesi* and *T. platensis* with a lower similar body mass (~ 1,900 kg) could be competitively excluded, thus forced to forage slightly more open environments including the woodlands and arboreal savannas, resulting in a more generalized diet.

Species with larger body mass have a more homogeneous spatial distribution than smaller ones, because their tolerance for lower quality resource consumption (i.e., fibrous foods with low protein content) allows them to use more diverse habitats, alleviating interspecific competition (Owen-Smith, 1992). Thus, the camelid *P. major* (~ 280 kg) that inhabited subcanopies had a possibly strictly folivorous diet, whereas the tapir *Tapirus* sp. (~ 250 kg) had a more diverse diet and the fruits were important dietary items, similar to cervid *Mazama* sp. (~ 40 kg). Although, the tapir possibly foraged more in denser forests and in areas close to water bodies such as igarapés or in floodplain (várzea) forest and rivers compared to the cervid. The pampatheriid *H. rondoniensis* (~ 120 kg) was also a browser in this region, but not restricted and could also feed on herbaceous from understories, and the giant capybara *Neochoerus* sp. (~ 200 kg) with similar diet behavior as the living *Hydrochoerus*, probably fed predominantly C_3 herbaceous and few C_4 grasses near water bodies.

Comparison of our data with several previous studies about the paleoecology of the analyzed specimens, permit to assume that resource partitioning and different behaviors in habitat use were the main mechanisms for reducing interspecific competition and the maintenance of the coexistence of large herbivorous mammal assemblages that inhabited the late Pleistocene of southwestern Amazon. Similarly, Dantas et al. (2017) were also

able to infer the structure of the assemblages, the partitioning and overlapping niches of the Pleistocene megamammals that inhabited the BIR, comparing the results of stable isotopes of carbon and oxygen with the current mammal assemblages of the Africa.

The megamammal species probably could have played important roles in the Amazon forest ecosystem during the late Quaternary, contributing for a greater habitat heterogeneity (i), because the herbivore pressure may vary across the space, resulting in a mosaic landscape (Malhi et al., 2016). Greater variation in floristic composition (ii), due to the large capacity of large fruit seed dispersal for greater distances than large modern ones as the tapirs, thus contributing to increased gene flow between plant populations (Guimarães et al., 2008). The megamammals could also contributes increasing the longevity of mature forest trees and higher forest biomass (iii), due to high pressure by consumption of the understory and subcanopies plants, which can reduce the below-ground competition for nutrients (Terborgh et al., 2015a, b), as well as by accelerating the ecosystem biogeochemical cycling (iv), because nutrients that would be locked for years in leaves and stems are liberated for use through animal consumption, digestion, defecation, and urination, and the nutrients in recalcitrant woody biomass are moved to the decomposition pool through breakage and plant mortality (Malhi et al., 2016).

5. Conclusions

The carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) stable isotope analyses aided in the comprehension of some aspects of feeding ecology and habitats of medium- and mega-herbivores mammals that inhabited the southwestern Amazon during the late Quaternary. The isotopic data together with previous paleoecological interpretations of the studied species, and some information regarding feeding behavior of living species allowed refining the interpretations about the diet and possible ecological interactions. According

to the $\delta^{13}C_{VPDB}$ (– 17.47‰ to – 8.83‰) and $\delta^{18}O_{VSMOW}$ (19.90 to 25.80 ‰) results, the Amazonian late Quaternary mammals inhabited heterogeneous forest habitats, which facilitated the resource partitioning and the use of distinct habitats. The mammal assemblages were composed mostly by browsers, with the only exception being the C_3 and C_4 generalists *Trigodonops lopesi* and *Neochoerus* sp. (p_iC_3 = ~ 70%; B_A = ~ 0.75). The largest bodied species, *Eremotherium laurillardi* and *Notiomastodon platensis*, were probably key species that structured the assemblages through ecosystem modelling, facilitating the access to resources by other large and middle-sized species (e.g., cingulates, tapirs, camelids and cervids), and limiting the abundance of other megamammal species through the competition for resources (e.g., toxodonts). Further paleoecological reconstructions are needed, in order to better understand the paleoenviromental scenarios and ecological interactions of the mammal species that inhabited the southwestern Amazon during the late Quaternary.

Acknowledgments

The authors are grateful to the grant by Academy of Finland for the Subamazon project, University of Turku, Finland (process number 296406) and the Universidade Federal do Acre, Rio Branco, Brazil for supporting travelling costs to access the fossil collections. J. C. Rabelo (Universidade Federal de Mato Grosso) for supporting the construction of fossiliferous localities map in Arcgis software. Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the doctoral scholarship granted to L. Asevedo (process number 88882.443670/2019-01). Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the financial support through Universal project (process number 404684/2016-5) and research fellowship for M.A.T. Dantas (PQ/CNPq 311003/2019-2). The authors are also thankful to the

anonymous reviewers for their valuable comments and suggestions for improving the quality of this paper.

6. References

Alberdi, M.T., Cerdeño, E., Prado, J.L., 2008. *Stegomastodon platensis*(Proboscidea, Gomphotheriidae) enel Pleistoceno de Santiago del Estero, Argentina. Ameghiniana. 45(2), 257-271.

Anderson, J. F., Hall- Martin, A., Russell, D. A., 1985. Long- bone circumference and weight in mammals, birds and dinosaurs. Journal of Zoology. 207(1), 53-61.

Arruda, D. M., Schaefer, C. E., Fonseca, R. S., Solar, R. R., Fernandes- Filho, E. I., 2018. Vegetation cover of Brazil in the last 21 ka: New insights into the Amazonian refugia and Pleistocenic arc hypotheses. Global Ecology and Biogeography. 27(1), 47-56.

Asevedo, L., Winck, G. R., Mothé, D., Avilla, L. S., 2012. Ancient diet of the Pleistocene gomphothere *Notiomastodon platensis* (Mammalia, Proboscidea, Gomphotheriidae) from lowland mid-latitudes of South America: Stereomicrowear and tooth calculus analyses combined. Quaternary International.255, 42-52.

Asevedo, L., D'Apolito, C., Misumi, S. Y., Barros, M. A., Barth, O. M., Avilla, L. S., 2020. Palynological analysis of dental calculus from Pleistocene proboscideans of southern Brazil: A new approach for paleodiet and paleoenvironmental reconstructions. Palaeogeography, Palaeoclimatology, Palaeoecology. 540, 109523.

Ayliffe, L.K., Lister, A.M., Chivas, A.R., 1992. The preservation of glacial-interglacial climatic signatures in the oxygen isotopes of elephant skeletal phosphate. Palaeogeography, Palaeoclimatology, Palaeoecology. 99, 179-191.

Badeck, F. W., Tcherkez, G., Nogues, S., Piel, C., Ghashghaie, J., 2005. Post-photosynthetic fractionation of stable carbon isotopes between plant organs—a

widespread phenomenon. Rapid Communications in Mass Spectrometry: An International Journal Devoted to the Rapid Dissemination of Up- to- the- Minute Research in Mass Spectrometry. 19 (11), 1381-1391.

Bargo, M. S., Toledo, N., Vizcaíno, S. F., 2006. Muzzle of South American Pleistocene ground sloths (Xenarthra, Tardigrada). Journal of Morphology. 267(2), 248-263.

Bodmer, R. E., 1990a. Responses of ungulates to seasonal inundations in the Amazon floodplain. Journal of tropical Ecology. 6 (2), 191–201.

Bodmer, R. E., 1990b. Fruit patch size and frugivory in the lowland tapir (*Tapirus terrestris*). Journal of Zoology. 222 (1), 121–128.

Bond, M., Cerdeño, E., López, G., 1997. Los ungulados nativos de América del Sur. In: Alberdi, M.T., Leone, G., Tonni, E.P. (Eds.), Evolución Biológica y Climática de la Region Pamapeana durante los Últimos Cinco Millones de Años. Monografías Museo Nacional de Ciencias Naturales, Madrid, pp. 257–275.

Borges, L. H. M., 2014. Abundância de mamíferos de médio e grande porte em resposta ao grau de distanciamento do rio Chandless, Parque Estadual Chandless, Acre, Brasil. Universidade Federal do Acre, Rio Branco, M.Sc. thesis, 69p.

Branan, W. V., Werkhoven, M. C., Marchinton, R. L., 1985. Food habits of brocket and white-tailed deer in Suriname. The Journal of wildlife management. 49, 972-976.

Bryant, J.D., Koch, P.L., Froelich, P.N., Showers, W.J., Genna, B.J., 1996. Oxygen isotope partitioning between phosphate and carbonate in mammalian apatite. Geochimica et Cosmochimica Acta. 60(24), 5145-5148.

Bush, M.B., Weimann, M., Piperno, D.R., Liu, K.K.B., Colinvaux, P.A., 1990. Pleistocene temperature depression and vegetation change in Ecuadorian Amazonia. Quaternary Research. 34, 330–45.

769 Bush, M.B., Oliveira, P.E., Colinvaux, P.A., Miller, M.C., Moreno, J.E., 2004.
770 Amazonian palaeoecological histories: One Hill, Three Watersheds.
771 Palaeogeography, Palaeoclimatology, Palaeoecology. 214, 359–93.
772 Cerling, T. E., Harris, J. M., 1999. Carbon isotope fractionation between diet and
773 bioapatite in ungulate mammals and implications for ecological and paleoecological
774 studies. Oecologia. 120(3), 347-363.
775 Cheng, H., Sinha, A., Cruz, F.W., Wang, X., Edwards, R.L., d'Horta, F.M., Ribas, C.C.,
776 Vuille, M., Stott, L.D., Auler, A.S., 2013. Climate change patterns in Amazonia
777 andbiodiversity. Nature communications. 4(1), 1-6.
778 Cherkinsky, A., 2009. Can we get a good radiocarbon age from “bad bone”? Determining
779 the reliability of radiocarbon age from bioapatite. Radiocarbon. 51-2, 647-655.
780 Cohen, M. C. L., Rossetti, D. F., Pessenda, L. C. R., Friaes, Y. S., Oliveira, P. E., 2014.
781 Late Pleistocene glacial forest of Humaitá-Western Amazonia. Palaeogeography,
782 Palaeoclimatology, Palaeoecology. 415, 37-47.
783 Colinvaux, P.A., Oliveira, P.E., Moreno, J.E., Miller, M.C., Bush, M.B., 1996. A long
784 pollen record from lowland Amazonia: forest and cooling in glacial times. Science.
785 274, 85–8.
786 Colinvaux, P.A., Oliveira, P.E., Bush, M.B., 2000. Amazonian and neotropical plant
787 communities on glacial time-scales: the failure of the aridity and refuge hypotheses.
788 Quaternary Science Reviews. 19, 141–69.
789 Colivaux, P.A., Irion, G., Räsänen, M.E., Bush, M.B., Mello, J.A.S.N., 2001. A paradigm
790 to be discarded: geological and paleoecological data falsify the Haffer and Prance
791 refuge hypothesis of Amazonian speciation. Amazoniana. 16, 609–46.
792 Coplen, T. B., 1994. Reporting of stable hydrogen, carbon, and oxygen isotopic
793 abundances (technical report). Pure and Applied Chemistry. 66(2), 273-276.

794 Corriale, M. J., Loponte, D., 2015. Use of stable carbon isotope ratio for foraging behavior
795 analysis of capybara (*Hydrochoerus hydrochaeris*) from Esteros del Iberá,
796 Argentina. MammalianBiology. 80(2), 73-80.
797 Dantas, M. A. T., Xavier, M. C. T., França, L.M., Cozzuol, M. A., Ribeiro, A.S.,
798 Figueiredo, A. M. G., Kinoshita, A., Baffa, O.,2013. A review of the time scale and
799 potential geographic distribution of *Notiomastodon platensis* (Ameghino, 1888) in
800 the late Pleistocene of South America. QuaternaryInternational. 317, 73-79.
801 Dantas, M. A. T., Cherkinsky, A., Bocherens, H., Drefahl, M., Bernardes, C., França, L.
802 M., 2017. Isotopic paleoecology of the Pleistocene megamammals from the Brazilian
803 Intertropical Region: Feeding ecology ($\delta^{13}C$), niche breadth and overlap. Quaternary
804 Science Reviews. 170, 152-163.
805 Dantas, M. A. T., 2019. Atualizando a estimativa da massa corporal da megafauna do
806 Pleistoceno Final da Região Intertropical Brasileira. In: XXVI Congresso Brasileira
807 de Paleontologia, Uberlândia, Minas Gerais, Brazil. Paleontologia em Destaque,
808 219-220p.
809 Dantas, M. A. T., Cherkinsky, A., Lessa, C. M. B., Santos, L.V., Cozzuol, M.A., Omena,
810 E.C., Silva, J.L.L., Sial, A.N., Bocherens, H., 2020. Isotopic Paleoecology ($\delta^{13}C$,
811 $\delta^{18}O$) of Late Quarternary megafauna from Brazilian Intertropical Region.Revista
812 Brasileira de Paleontologia, v. 23, n 2.
813 De Iuliis, G., Bargo, M. S., Vizcaíno, S. F., 2001. Variation in skull morphology and
814 mastication in the fossil giant armadillos Pampatherium spp. and allied genera
815 (Mammalia: Xenarthra: Pampatheriidae), with comments on their systematics and
816 distribution. Journal of Vertebrate Paleontology. 20(4), 743-754.

817 Domingo, L., Prado, J.L., Alberdi, M.T., 2012. The effect of paleoecology and
818 paleobiogeography on stable isotopes of Quaternary mammals from South America.
819 Quaternary Sciences Review. 55, 103-113.
820 Duarte, J. M. B., Jorge, W., 1996. Chromosomal polymorphism in several populations of
821 deer (genus Mazama) from Brazil. Archivos de Zootecnia. 45, 281-287.
822 Ehleringer, J.R., Cerling, T.E., 2002. C3 and C4 photosynthesis. In: Mooney, H.A.,
823 Canadell, J.G. (Eds.), The earth system: biological and ecological dimensions of
824 global environmental change. Chichester: John Wiley & Sons, Ltd, v. 2, p. 186–90.
825 Eisenberg, J.F., Redford, K.M., 1999. Mammals of the Neotropics: The central
826 Neotropics. Chicago, University of Chicago Press.
827 Emmons, L.H., Feer, F., 1997. Neotropical rainforest mammals: A field guide. 2 ed.
828 Chicago: The University of Chicago Press.
829 Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using
830 the abrasion-attrition wear gradient: a new method for reconstructing
831 paleodiets. American Museum Novitates. 2000(3301), 1-36.
832 Fragoso, J. M., Huffman, J. M., 2000. Seed-dispersal and seedling recruitment patterns
833 by the last Neotropical megafaunal element in Amazonia, the tapir. Journal of
834 Tropical Ecology. 16(3), 369-385.
835 Fragoso, J. M., Silvius, K. M., Correa, J. A., 2003. Long- distance seed dispersal by tapirs
836 increases seed survival and aggregates tropical trees. Ecology. 84(8), 1998-2006.
837 França, L. M., Dantas, M. A. T., Bocchiglieri, A., Cherckinsky, A., Ribeiro, A. S.,
838 Bocherens, H., 2014. Chronology and ancient feeding ecology of two upper
839 Pleistocene megamammals from the Brazilian Intertropical Region. Quaternary
840 Science Reviews. 99, 78-83.

841 Freitas, H. A., Pessenda, L. C. R., Aravena, R., Gouveia, S. E. M., Ribeiro, A. S., Boulet,
842 R., 2001. Late Quaternary vegetation dynamics in the southern Amazon basin
843 inferred from carbon isotopes in soil organic matter. Quaternary Research. 55(1), 39-
844 46.
845 Fricke, H., 2007. Stable Isotope Geochemistry of Bonebed Fossils: Reconstructing
846 Paleoenvironments, Paleoecology, and Paleobiology. In: Rogers, R.R., Eberth, D.A.,
847 Fiorillo, A.R. (Eds.). Bonebeds: Genesis, Analysis, and Paleobiological Significance.
848 The University of Chicago Press, p. 437-490.
849 Fritz, H., Duncan, P., Gordon, I.J., Illius, A.W., 2002. Megaherbivores influence trophic
850 guilds structure in African ungulate communities. Oecologia. 131, 620-625.
851 Gayot, M., Henry, O., Dubost, G., Sabatier, D., 2004. Comparative diet of the two forest
852 cervids of the genus Mazama in French Guiana. Journalof Tropical Ecology. 20(1),
853 31-43.
854 Ghizzoni, M., 2014. Estimación de lamasa corporal de
855 unejemplarcuaternariodelcarpincho extinto *Neochoerus* a través de medidas cráneo-
856 dentales. Revista Brasilera Paleontologia. 17, 83-90.
857 Góis, F., Nascimento, E. D., Porto, A. S., Holanda, E. C., Cozzuol, M. A., 2004.
858 Ocorrências de Cingulata dos gêneros *Kraglievichia* e *Holmesina* do Terciário e
859 Quaternário da Amazônia Sul-Ocidental. Ameghiniana. 41(4), 49R.
860 Guimarães Jr, P. R., Galetti, M., Jordano, P., 2008. Seed dispersal anachronisms:
861 rethinking the fruits extinct megafauna ate. PloSone, 3(3), e1745.
862 Gutiérrez, M., Alberdi, M. T., Prado, J. L., Perea, D., 2005. Late Pleistocene
863 *Stegomastodon* (Mammalia, Proboscidea) from Uruguay. Neues Jahrbuch fur
864 Geologie und Palaontologie-Monatshefte. 11, 641-662.
865 Haffer, J., 1969. Speciation in Amazonian forest birds. Science 165, 131–7.

866 Higgins, P., 2018. Isotope ecology from biominerals. In: D. A. Croft, D. F. Su, S. W.
867 Simpson (Eds.), Methods in paleoecology: Reconstructing Cenozoic terrestrial
868 environments and ecological communities. Springer, p. 99 –120.
869 Holanda, E. C., Cozzuol, M. A., 2006. New records of *Tapirus* from the late Pleistocene
870 of southwestern Amazonia, Brazil. Revista Brasileira de Paleontologia. 9(2), 193-
871 200.
872 Holanda, E. C., Ferigolo, J., Ribeiro, A. M., 2011. New *Tapirus* species (Mammalia:
873 Perissodactyla: Tapiridae) from the upper Pleistocene of Amazonia,
874 Brazil. JournalofMammalogy. 92(1), 111-120.
875 IBGE. Manual Técnico da Vegetação Brasileira. Rio de Janeiro, 2012.
876 Irion, G., Bush, M.B., Mello, J.A.N., Stüben, D., Neumann, T., Müller, R.G., Moraes,
877 J.O., Junk, J.W., 2006. A multiproxy palaeoecological record of Holocene lake
878 sediments from the Rio Tapajós, eastern Amazonia. Palaeogeography,
879 Palaeoclimatology, Palaeoecology. 240, 523–36.
880 Keeling, C. D., 1979. The Suess effect: ^{13}Carbon-^{14}Carbon interrelations. Environment
881 International. 2 (4-6), 229-300.
882 Koch, P.L., 2007. Isotopic study of the biology of modern and fossil vertebrates. In:
883 Michener, R., Lajtha, K. (eds.). Stable Isotopes in Ecology and Environmental
884 Science. 2a edição. Blackwell Publishing, p. 99-154.
885 Kohn, M. J., 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of
886 (paleo) ecology and (paleo) climate. Proceedings of the National Academy of
887 Sciences. 107(46), 19691-19695.
888 Latrubesse, E. M., Rancy, A., 1998. The late Quaternary of the Upper Juruá River,
889 southwestern Amazonia, Brazil: geology and vertebrate paleontology. Quaternary of
890 South America and Antarctic Peninsula. 11(2), 27-46.

Ledru, M.P., 2002. Late Quaternary history and evolution of the cerrados as revealed by palynological records. In: Oliveira PS, Marquis RJ, editors. The Tropical Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. New York:University Press. p 33–52.

Ledru, M. P, Ceccantini, G., Gouveia, S.E.M., López-Sáez, J.A., Pessenda, L.C.R., Riberito, A.S., 2006. Millenialscale climatic and vegetation changes in a northern Cerrado (Northeast, Brazil) since the Last Glacial Maximum. Quaternary Science Reviews. 25,1110–26.

Levin, N. E., Cerling, T. E., Passey, B. H., Harris, J. M., Ehleringer, J. R., 2006. A stable isotope aridity index for terrestrial environments. Proceedings of the National Academy of Sciences. 103(30), 11201-11205.

Levins, R., 1968. Evolution in changing environments: some theoretical explorations. New Jersey, Princeton University Press, No. 2, 120p.

Liu, K.B, Colinvaux, P.A., 1985. Forest changes in the Amazon Basin during the last glacial maximum. Nature. 318, 556–7.

Lopes, R. P., Ribeiro, A. M., Dillenburg, S. R., Schultz, C. L., 2013. Late middle to late Pleistocene paleoecology and paleoenvironments in the coastal plain of Rio Grande do Sul State, Southern Brazil, from stable isotopes in fossils of *Toxodon* and *Stegomastodon*. Palaeogeography, Palaeoclimatology, Palaeoecology.369, 385-394.

MacFadden, B. J., Higgins, P., 2004. Ancient ecology of 15-million-year-old browsing mammals within C3 plant communities from Panama. Oecologia. 140(1), 169-182.

MacFadden, B. J., 2005. Diet and habitat of toxodont megaherbivores (Mammalia, Notoungulata) from the late Quaternary of South and Central America. Quaternary Research. 64(2), 113-124.

915 Marcolino, C. P., Isaias, R. M. S., Cozzuol, M. A., Cartelle, C., Dantas, M. A. T., 2012.
916 Diet of *Palaeolama major* (Camelidae) of Bahia, Brazil, inferred from
917 coprolites. Quaternary International. 278, 81-86.
918 Marshall, J.D., Brooks, J.R., Lajtha, K., 2007. Sources of variation in the stable isotopic
919 composition of plants. In: Michener, R., Lajtha, K. (eds.). Stable Isotopes in Ecology
920 and Environmental Science. 2a edição. Blackwell Publishing, p. 22-60.
921 Mayle, F.E., Power, M.J., 2008. Impact of a drier Early–Mid-Holocene climate upon
922 Amazonian forests. PhilosophicalTransactionsofthe Royal Society B. 363,1829–38.
923 Mendonça, R., 2012. Diversidade de toxodontes pleistocênicos (Notoungulata,
924 Toxodontidae): uma nova visão. Universidade de São Paulo, Doctoralthesis, 151p.
925 Mosblech, N.A.S., Bush, M.B., Gosling, W.D., Hodell, D., Thomas, L., van Calsteren,
926 P., Correa-Metrio, A., Valencia, B.G., Curtis, J., van Woesik, R., 2012. North
927 Atlantic forcing of Amazonian precipitation during the last ice age.
928 NatureGeoscience. 5(11), 817-820.
929 Mothé, D., Avilla, L. S., Asevedo, L., Borges-Silva, L., Rosas, M., Labarca-Encina, R.,
930 Souberlich, R.,Soibelzon, E., Roman-Carrion, J. L., Ríos, S. D., Rincon, A. D.,
931 Oliveira, G. C., Lopes, R. P., 2017. Sixty years after 'The mastodonts of Brazil': The
932 state of the art of South American proboscideans (Proboscidea,
933 Gomphotheriidae). Quaternary International. 443, 52-64.
934 Naples, V. L., McAfee, R. K., 2012. Reconstruction of the cranial musculature and
935 masticatory function of the Pleistocene panamerican ground sloth *Eremotherium*
936 *laurillardi* (Mammalia, Xenarthra, Megatheriidae). Historical Biology. 24(2), 187-
937 206.
938 Nascimento, E. R., 2008. Os Xenarthra Pilosa (Megatheriidae), Notoungulata
939 (Toxodontidae) e Proboscidea (Gomphotheriidae) da Formação Rio Madeira,

940 Pleistoceno superior, Estado de Rondônia, Brasil. Universidade Federal do Rio
941 Grande do Sul, M.Sc. thesis, 113p.
942 Nelson, S. V., 2013. Chimpanzee fauna isotopes provide new interpretations of fossil ape
943 and hominin ecologies. Proceedings of the Royal Society B: Biological
944 Sciences. 280(1773), 20132324.
945 Oliveira, J. F., Asevedo, L., Cherkinsky, A., Dantas, M. A. T., 2020. Radiocarbon dating
946 and integrative paleoecology ($\delta^{13}C$, stereomicrowear) of *Eremotherium laurillardi*
947 (Lund, 1842) from midwest region of the Brazilian intertropical region. Journal of
948 South American Earth Sciences, 102653.
949 Olivier, J., Otto, T., Roddaz, M., Antoine, P. O., Londoño, X., Clark, L. G., 2009. First
950 macrofossil evidence of a pre-Holocene thorny bamboo cf. *Guadua* (Poaceae:
951 Bambusoideae: Bambuseae: Guaduinae) in south-western Amazonia (Madre de
952 Dios—Peru). Review of Palaeobotany and Palynology. 153(1-2), 1-7.
953 Owen-Smith, N., 1992. Megaherbivores: The influence of very large body size on
954 Ecology. Cambridge Univ Press, Cambridge, UK.
955 Padilla, M., Dowler, R.C., 1994. Tapirusterrestris. Mammalian Species: American
956 Society of Mammalogists. N 481. Northampton. 1-8 p.
957 Pansani, T. R., Muniz, F. P., Cherkinsky, A., Pacheco, M. L. A. F., Dantas, M. A. T.,
958 2019. Isotopic paleoecology ($\delta^{13}C$, $\delta^{18}O$) of Late Quaternary megafauna from Mato
959 Grosso do Sul and Bahia States, Brazil. Quaternary Science Reviews. 221,
960 105864.Parssinen, M., Balee, W., Ranzi, A., Barbosa, A., in press. Evidence of 10
961 000-year-old human land-use practices, fires and climate in the geoglyph sites of
962 Southwestern Amazonia. Antiquity.

963 Paula Couto, 1982. Fossil mammals from the Cenozoic of Acre, Brasil. V-
964 NotoungulataNesodontinae (II), Toxodontidae and Haplodontiinae, and Litopterna,
965 Pyrotheria and Astrapotheria (II). Iheringia. Sério geologia. N 7, P 5
966 Paula-Couto, C. D., 1983a. Fossil mammals from the Cenozoic of Acre, Brazil, VI–
967 EdentataCingulata. Iheringia, Série Geologia, 8, 33-49.
968 Paula Couto, C. P., 1983b. Fossil Mammals from the Cenozoicof acre Brasil. vii–
969 Miscellanea. Iheringia Série Geologia Porto Alegre, 8, 101-120.
970 Pessenda, L. C. R., Gomes, B. M., Aravena, R. R. A. S., Ribeiro, A. D. S., Boulet, R.,
971 Gouveia, S. E. M., 1998. The carbon isotope record in soils along a forest-cerrado
972 ecosystem transect: implications for vegetation changes in the Rondonia state,
973 southwestern Brazilian Amazon region. The Holocene. 8(5), 599-603.
974 Phillips, D. L., 2012. Converting isotope values to diet composition: the use of mixing
975 models. Journal of Mammalogy. 93(2), 342-352.
976 Pianka, E. R., 1973. The structure of lizard communities. Annual review of ecology and
977 systematics. 4(1), 53-74.
978 Porto, A. S., Góis, F., Nascimento, E. D., Holanda, E. C., Cozzuol, M. A., 2004. Xenarthra
979 Pilosa (Edentata) do Quaternário do Estado de Rondônia. Ameghiniana
980 Suplemento. 41, 60R.
981 Ranzi, A., 2000. Paleoecologia da Amazônia: megafauna do Pleistoceno. Florianópolis:
982 EDUFSC, 2000. 101 p.
983 Ranzi, A., 2008. Paleontologia da Amazônia: mamíferos fósseis do Juruá. Rio Branco:
984 M.M. Paim Representações e Comércio. 130 p.
985 Redford, K.H., Eisenberg, J.F., 1992. Mammals of the Neotropics: The southern cone.
986 Chicago, University of Chicago Press.

Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Haflidason, H., Hajdas, I., Hatt_e, C., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kaiser, K.F., Kromer, B., Manning, S.W., Niu, M., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Turney, C.S.M., Van der Plicht, J., 2013. IntCal13 and MARINE13 radiocarbon age calibration curves 0-50000 years calBP. Radiocarbon 55 (4), 1869e1887

Rizzotto, G. J., De Oliveira, J.G.F., 2005. Projeto Rio Madeira - levantamento de informações para subsidiar o estudo de viabilidade do aproveitamento hidroelétrico (AHE) do Rio Madeira. Relatório Final. CPRM–Serviço Geológico do Brasil, Porto Velho, Brazil.

Rossetti, D. F., Cohen, M. C., Pessenda, L. C., 2017. Vegetation change in Southwestern Amazonia (Brazil) and relationship to the late Pleistocene and Holocene climate. Radiocarbon, 59 (1), 69-89.

Sánchez, B., Prado, J. L., Alberdi, M. T., 2004. Feeding Ecology, dispersal, and extinction of South American Pleistocene gomphotheres (Gomphotheriidae, Proboscidea). Paleobiology. 30 (1), 146-161.

Scillato-Yané, G. J., Carlini, A. A., Tonni, E. P., Noriega, J. I., 2005. Paleobiogeography of the late Pleistocene pampatheres of South America. Journal of South American Earth Sciences. 20(1-2), 131-138.

Simpson, G.G., Paula Couto, C., 1981. Fossil mammals from the Cenozoic of Acre, Brazil III - Pleistocene Edentata Pilosa, Proboscidea, Sirenia, Perissodactyla and Artiodactyla. Iheringia. Série geologia. N 6, P 11-73.

1010 Solounias, N., Semprebon, G., 2002. Advances in the reconstruction of ungulate
1011 ecomorphology with application to early fossil equids. American
1012 MuseumNovitates. 2002(3366), 1-49.
1013 Sponheimer, M., Lee-Thorp, J. A., 1999. Oxygen isotopes in enamel carbonate and their
1014 ecological significance. Journal of Archaeological Science. 26(6), 723-728.
1015 Tejada-Lara, J. V., MacFadden, B. J., Bermudez, L., Rojas, G., Salas-Gismondi, R.,
1016 Flynn, J. J., 2018. Body mass predicts isotope enrichment in herbivorous
1017 mammals. Proceedings of the Royal Society B: Biological Sciences. 285(1881),
1018 20181020.
1019 Tejada, J. V., Flynn, J. J., Antoine, P. O., Pacheco, V., Salas-Gismondi, R., Cerling, T.
1020 E., 2020. Comparative isotope ecology of western Amazonian rainforest
1021 mammals. Proceedings of the National Academy of Sciences. 117(42), 26263-
1022 26272.
1023 Terborgh, J., Davenport, L.C., 2015a. Megafaunal influences on tree recruitment in
1024 African equatorial forests. Ecography (Cop), 10.1111/ecog.01641.
1025 Terborgh J., et al., 2015b. The African rainforest: Odd man out or megafaunal landscape?
1026 African and Amazonian forests compared. Ecography. 39,187 193.
1027 van Breukelen, M. R., Vonhof, H. B., Hellstrom, J. C., Wester, W. C. G., Kroon, D., 2008.
1028 Fossil dripwater in stalagmites reveals Holocene temperature and rainfall variation
1029 in Amazonia. Earth and Planetary Science Letters. 275, 54–60.
1030 van der Hammen, T., Absy, M.L., 1994. Amazonia during the last glacial.
1031 Palaeogeography, Palaeoclimatology, Palaeoecology. 109, 247–61.
1032 van der Hammen, T., Hooghiemstra, H., 2000. Neogene and Quaternary history
1033 ofvegetation, climate and plant diversity in Amazonia. Quaternary Science Reviews.
1034 19, 725–42.

van der Merwe, N. J., Medina, E., 1991. The canopy effect, carbon isotope ratios and foodwebs in Amazonia. Journal of Archaeological Science. 18(3), 249-259.

Viana, M.S.S., Silva, J.L.L., Oliveira, P.V., Julião, M.S.S., 2011. Hábitos alimentares em herbívoros da megafauna pleistocênica no nordeste do Brasil. Estudos Geológicos. 21 (2), 89–95.

Vizcaíno, S. F., De Iuliis, G., Bargo, M. S., 1998. Skull shape, masticatory apparatus, and diet of *Vassallia* and *Holmesina* (Mammalia: Xenarthra: Pampatheriidae): when anatomy constrains destiny. Journal of Mammalian Evolution. 5(4), 291-322.

Yann, L. T., DeSantis, L. R., Haupt, R. J., Romer, J. L., Corapi, S. E., Ettenson, D. J., 2013. The application of an oxygen isotope aridity index to terrestrial paleoenvironmental reconstructions in Pleistocene North America. Paleobiology. 39(4), 576-590.

Figure captions

Fig. 1. Localities of the late Quaternary mammals from southwestern Amazon ~~at~~ along the banks of Juruá (locality 1, a-d) and Chandless rivers (locality 2) in Acre state, as also in Araras locality, Madeira R~~r~~iver (locality 3) in Rondônia state, Brazil. The l~~L~~ocalities of *Toxodon platensis* from Peru and Bolivia (localities 4-9) are from Macfadden (2005).

Fig. 2. Bivariate plot with $\delta^{13}C_{VPDB}$ and $\delta^{18}O_{VSMOW}$ values from late Quaternary herbivorous mammals of the southwestern Amazonia. The enrichment ranges of $\delta^{13}C$ values were according to the body mass by Tejada-Lara et al. (2018). A) species with body mass > 3,500 kg (ε^* = 15 ‰). B) species with body mass between 3,500 to 600 kg (ε^* = 14 ‰). C) species with body mass between 600 to 75 kg and < 75 kg (ε^* = 13 and

12 ‰, respectively). The traces represent the average of $\delta^{13}C$ values for C_3 and C_4 resources.

Fig. 3. Reconstruction of late Quaternary herbivorous mammals from southwestern Amazon in distinct phytodomains. A) *Tapirus* sp., *Palaeolama major*, *Notiomastodon platensis* and *Eremotherium laurillardi* (from left to right) in closed-canopy forest habitat. B) *Holmesina rondoniensis*, *Toxodon platensis* and *Mazama* sp. (from left to right) in mesic woodland, and C) *Neochoerus* sp. and *Trigodonops lopesi* in arboreal savanna habitat. Artist Beatriz Grigio.

Fig. 4. Box-plot of $\delta^{13}C_{VPDB}$ values for the Pleistocene megaherbivores species *Eremotherium laurillardi* (A), *Notiomastodon platensis* (B), *Toxodon platensis* and *Trigodonops lopesi* (C) from southwestern Amazon compared to different ecoregions from South America. Abbreviation: Tri = *Trigodonops lopesi*. Ecoregions: Brazilian Intertropical Region (= BIR; Northeast, Midwest and Southeast of Brazil; Sánchez et al., 2004; Macfadden, 2005; Viana et al., 2011; Dantas et al., 2013, França et al., 2014; Pansani et al., 2019; Dantas et al., 2017), Andes~~an~~ (Ecuador and Peru; Sánchez et al., 2004; Domingo et al., 2012), Chaco (Bolivia an Argentina; Macfadden, 2005; Alberdi et al., 2008; Domingo et al., 2012) and Pampa (Argentina, Uruguay and Brazil; Sánchez et al., 2004; Macfadden, 2005; Gutiérrez et al., 2005; Domingo et al., 2012; Lopes et al., 2013).

Table caption

Table 1. Mean values of $\delta^{13}C_{VPDB}$ and $\delta^{18}O_{VSMOW}$, proportional contributions of diet sources (*pi*C_3 plants, *pi*C_4 plants) and standardized isotopic niche breadth (B_A) from Quaternary mammal assemblages of southwestern Amazon. A) Araras, Madeira River,

Rondônia state, B) Upper Juruá and Chandless rivers, Acre state, Brazil, C) and D) localities of Bolivia and Peru, respectively from Macfadden (2005). Acronym: BM = Body mass. References: a: Dantas et al. (2020), b: Dantas (2019), c: Padilla and Dowler (1994), d: Ghizzoni (2014), e: Duarte and Jorge (1996).

Table 2. Values of $\delta^{18}O_{P\text{-}VSMOW}$ and $\delta^{18}O_{mwVSMOW}$ obtained from oxygen isotopes in carbonate enamel ($\delta^{18}O_C$) of *Notiomastodon platensis* from southwestern Amazon.

Supplementary material

Supplementary Table 1. Summary data of $\delta^{13}C_{VPDB}$ and $\delta^{18}O_{VSMOW}$ values and ^{14}C AMS datings of Quaternary mammal species from southwestern Amazon. Abbreviations: E = enamel, D = dentine and B = bone. Carbon and oxygen isotope data of *Toxodon platensis* from Peru and Bolivia by Macfadden (2005).

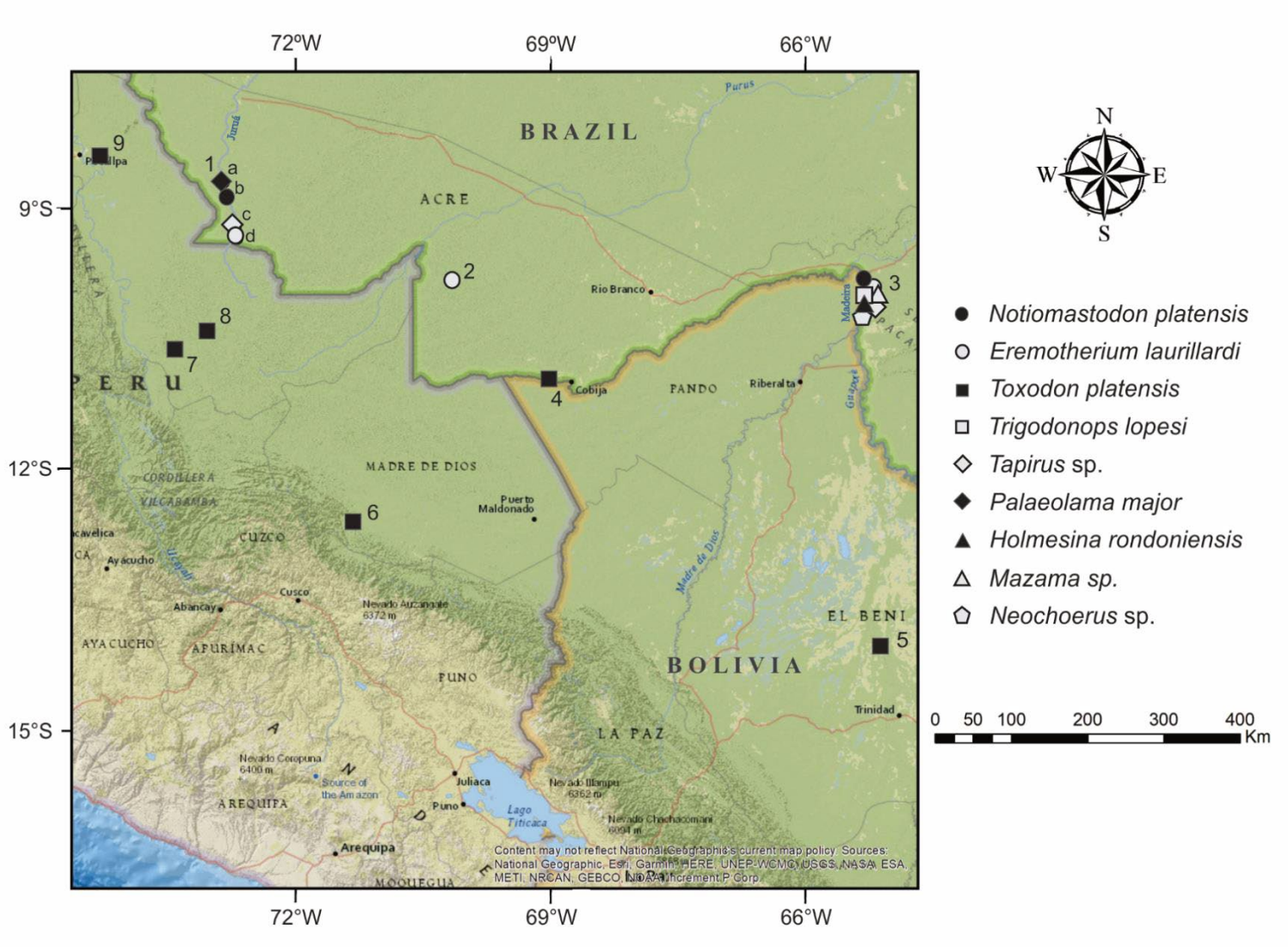
72°W
69°W
66°W
9°S
12°S
15°S
BRAZIL
ACRE
PERU
MADRE DE DIOS
PANDO
EL BENI
BOLIVIA
CUZCO
AYACUCHO
APURÍMAC
PUNO
LA PAZ
AREQUIPA
MOQUEGUA
Rio Branco
Cobija
Riberalta
Puerto Maldonado
Cusco
Ayacucho
Abancay
Arequipa
Juliaca
Puno
Trinidad
Nevado Ausangate 6372 m
Nevado Coropuna 6400 m
Nevado Illampu 6362 m
Nevado Chachacomani 6094 m
Source of the Amazon
Lago Titicaca
Madeira
Purus
Madre de Dios
Ucayali
CORDILLERA VILCABAMBA
Content may not reflect National Geographic's current map policy. Sources: National Geographic, Esri, Garmin, HERE, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, increment P Corp.
N
W
E
S
Notiomastodon platensis
Eremotherium laurillardi
Toxodon platensis
Trigodonops lopesi
Tapirus sp.
Palaeolama major
Holmesina rondoniensis
Mazama sp.
Neochoerus sp.
0 50 100 200 300 400
Km

Fig. 1

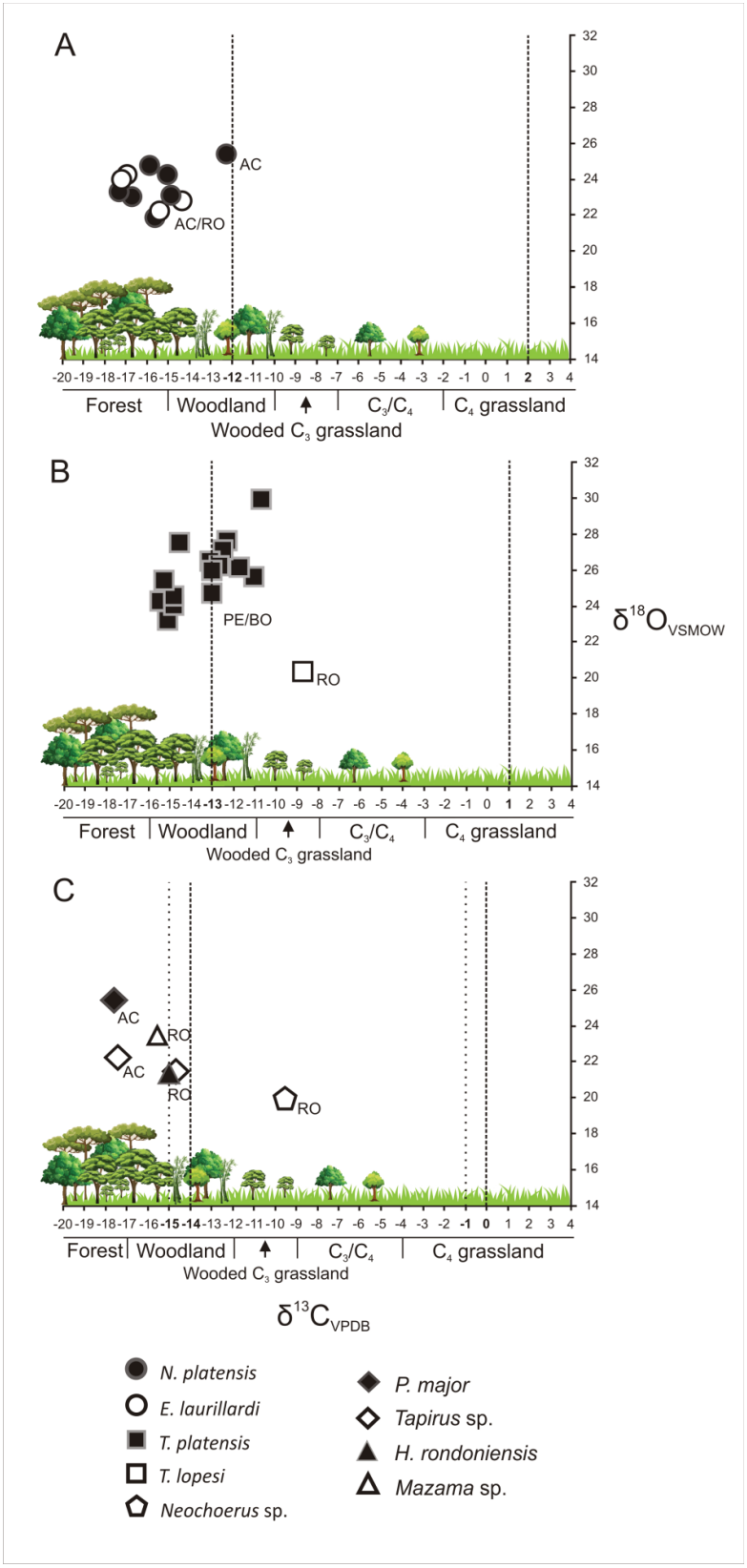
A
AC
AC/RO
B
PE/BO
RO
C
AC
RO
AC
RO
RO
Forest
Woodland
C3/C4
C4 grassland
Wooded C3 grassland
δ18OVSMOW
δ13CVPDB
N. platensis
E. laurillardi
T. platensis
T. lopesi
Neochoerus sp.
P. major
Tapirus sp.
H. rondoniensis
Mazama sp.

Fig. 2

Fig. 3A

Fig. 3B

Fig. 3C

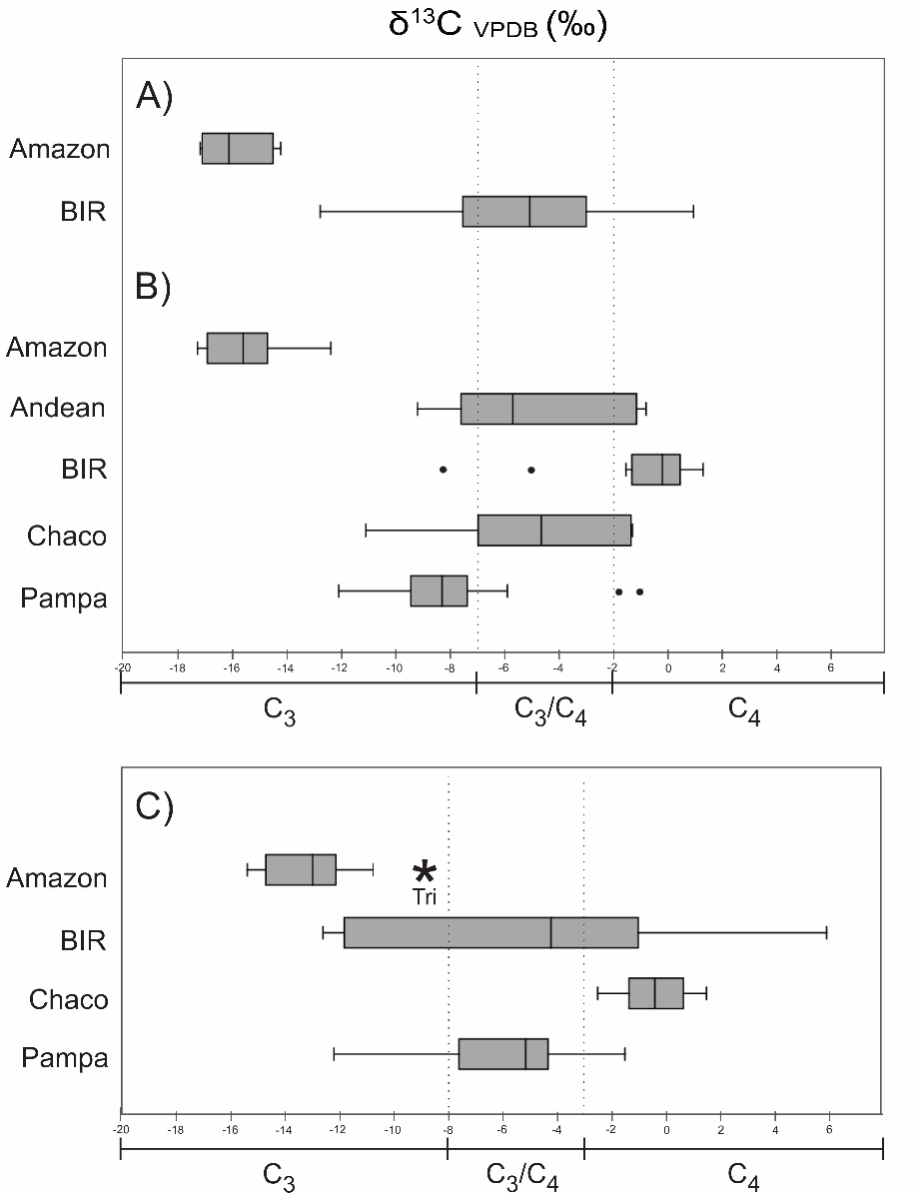
δ13C VPDB (‰)
A)
Amazon
BIR
B)
Amazon
Andean
BIR
Chaco
Pampa
-20 -18 -16 -14 -12 -10 -8 -6 -4 -2 0 2 4 6
C3
C3/C4
C4
C)
Amazon
*
Tri
BIR
Chaco
Pampa
-20 -18 -16 -14 -12 -10 -8 -6 -4 -2 0 2 4 6
C3
C3/C4
C4

Fig. 4

Table 1.

Species	BM (~Kg)	n	δ^{13}C ‰VPDB	p_iC3	p_iC4	B_A	δ^{18}O ‰VSMOW
A)							
E. laurillardi	3,500 [a]	1	− 14.23	1.00	0.00	0.00	22.72
N. platensis	6,300[a]	5	− 15.9 ± 1.2	1.00	0.00	0.00	23.07 ± 0.9
T. lopesi	1,900[b]	1	− 8.83	0.70	0.30	0.72	20.29
*Tapirus*sp.	250[c]	1	− 14.77	1.00	0.00	0.00	21.30
H. rondoniensis	120 [a]	1	− 14.89	1.00	0.00	0.00	21.37
Neochoerus sp.	200 [d]	1	− 9.66	0.69	0.31	0.75	19.90
Mazama sp.	40 [e]	1	− 15.47	1.00	0.00	0.00	23.57
B)							
E. laurillardi	3,500 [a]	3	− 16.5 ± 1.0	1.00	0.00	0.00	23.31 ± 1.1
N. platensis	6,300 [a]	2	− 14.1 ± 2.4	1.00	0.00	0.00	24.95 ± 0.5
P. major	280[a]	1	− 17.47	1.00	0.00	0.00	25.80
*Tapirus*sp.	250[c]	1	− 17.33	1.00	0.00	0.00	22.80
C)							
T. platensis	1,800[a]	5	− 13.9 ± 1.6	≥ 0.86	≤ 0.14	≤ 0.32	25.11 ± 1.6
D)							
T. platensis	1,800[a]	12	− 13.2 ± 1.4	≥ 0.84	≤ 0.16	≤ 0.38	26.05 ± 1.6

Table 2.

Colection code	Locality	δ^{18}Op‰	δ^{18}Ow‰
MERO ARQ 016	Madeira River, RO	14.46	-9.40
MERO PV 132 e 136	Madeira River, RO	14.73	-9.12
MERO PV 138	Madeira River, RO	12.96	-10.99
UFAC 1214	Madeira River, RO	14.21	-9.67
UFAC 4408	Madeira River, RO	15.51	-8.29
UFAC 104	Juruá River, AC	15.91	-7.86
UFAC PV 95	Juruá River, AC	16.58	-7.15

Supplementary Table 1.

Species	Colectioncode	Sample	Locality	$\delta^{13}C$ ‰$_{VPDB}$	$\delta^{18}O$ ‰$_{VSMOW}$	Calibrated Age (^{14} C)
Notiomastodon platensis	MERO ARQ 016	E	Araras, Madeira River, Nova Mamoré, Rondônia	−16.93	23.16	
	MERO PV 132 e 136	E	Araras, Madeira River, Nova Mamoré, Rondônia	−17.29	23.43	
	MERO PV 138	E	Araras, Madeira River, Nova Mamoré, Rondônia	−15.61	21.66	
	UFAC PV 1214	E	Araras, Madeira River, Nova Mamoré, Rondônia	−14.72	22.91	
	UFAC PV 4408	E	Araras, Madeira River, Nova Mamoré, Rondônia	−14.95	24.21	
	UFAC PV 104	E	Pedra Preta, Juruá River, Acre	−15.83	24.61	25,454 - 24,884
	UFAC PV 95	E	Pedra Preta, Juruá River, Acre	−12.39	25.28	
Eremotherium laurillardi	MERO PV 059	B	Araras, Madeira River, Nova Mamoré, Rondônia	−14.23	22.72	
	UFAC PV 98	B	Arenal, Juruá River, Cruzeiro do Sul, Acre	−16.90	24.09	
	EL 06 s/cod	B	Juruá River, Acre	−17.19	23.77	
	UFAC PV 6450	B	ChandlersRiver, Acre	−15.37	22.07	11,320 - 11,131
Palaeolama major	UFAC PV 061	D	Igarapé São Luis, Juruá River, Acre	−17.47	25.80	
*Tapirus*sp.	UFAC PV 035	B	Torre da Lua, Juruá River, Cruzeiro do Sul, Acre	−17.33	22.28	
Homelsinarondoniensis	MERO-P-002	B	Araras, Madeira River, Nova Mamoré, Rondônia	−14.89	21.37	
Neochoerus sp.	MERO (no code)	D	Araras, Madeira River, Nova Mamoré, Rondônia	−9.66	19.90	29,072 - 27,713
Mazama sp.	UFAC PV 4435B	B	Araras, Madeira River, Nova Mamoré, Rondônia	−15.47	23.57	
Trigodonopslopesi	MERO PV 100	D	Araras, Madeira River, Nova Mamoré, Rondônia	−8.83	20.29	

Species	Colectioncode	Sample	Locality	‰VPDB	$\delta^{18}O$ ‰VSMOW
Toxodon platensis	U-C1010	E	Beni-Yucuma-Maracas, Bolivia	− 11.00	
	U-C1011	E	Beni-Yucuma-Maracas, Bolivia	− 15.10	
	U-C1019-20	E	Beni-Yucuma-Maracas, Bolivia	− 14.70	
	U-C1012	E	Pando-Cobija, Bolivia	− 14.00	
	U-C1013	E	Pando-Cobija, Bolivia	− 14.50	
	U-C1018	E	Madre de Dios, Peru	− 13.00	
	F-04-001	E	InuyaRiver, Peru	− 12.50	
	F-04-002	E	InuyaRiver, Peru	− 10.70	
	F-04-003	E	InuyaRiver, Peru	− 12.70	
	F-04-004	E	InuyaRiver, Peru	− 11.70	
	F-04-005	E	PisquiRiver, Ucayali, Peru	− 15.30	
	F-04-006	E	Mapuya, Peru	− 12.30	
	F-04-007	E	Mapuya, Peru	− 13.00	
	F-04-008	E	Mapuya, Peru	− 12.80	
	F-04-009	E	Mapuya, Peru	− 15.40	
	F-04-010	E	Mapuya, Peru	− 14.10	
	F-04-011	E	Contamana, Peru	− 14.80	